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Frost hardiness of some New Zealand shrubs

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Title: Frost hardiness of some New Zealand shrubs
(Frosthärdighet hos några nyzeeländska buskar)

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Title page photos by author:
Large: *Olearia odorata* with tiny flowers in Gothenburg botanic garden.
Upper left: *Olearia* x *macrodonta* flowering
Middle left: *Podocarpus nivalis* with fruit
Lower left: *Coprosma acerosa* var. *brunnea* ‘Blue Beauty’ with fruit

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Summary

Frost resistances, LT_{50}, were decided for stems and leaves of several New Zealand woody plants belonging to *Olearia* (Asteraceae), *Coprosma* (Rubiaceae) and *Podocarpus* (Podocarpaceae). That was part of the aims, which included trying to find species potentially winter hardy in southern coastal Sweden and study methods for frost hardiness assessment. Artificial freeze tests were conducted in Sweden in late November 2006 and mid January 2007. Plants had hardened in cool temperatures (ca 5-10°C) and natural day lengths. Frost resistances were as expected found to be rather poor for New Zealand material (often between –8 and –13°C) compared to European reference material like *Taxus baccata* and *Buxus sempervirens* 'Rotundifolia' (often resistant to –20°C). The resistance measured in twigs of *Olearia odorata*, which topped all the New Zealand species with about –20°C was less expected, but reasonable considering it has been growing in the rock garden of Gothenburg botanic garden for three decades. Twig tissues of subalpine *Podocarpus* tested showed resistances of between –16 and –20°C in January, ranking them after the former. They are thought to be winter hardy in southern coastal Sweden, in the meaning they will survive there. Field observations are however needed to evaluate winter hardiness. Other findings including leaves were often of similar or poorer frost resistance compared to stems; in many species there were an increase of frost resistance from late November to mid January (Northern Hemisphere); and there was some correlation between the altitudinal distribution of the species and their frost resistances. In the method used, excised shoots were artificially frozen to a series of target temperatures, and evaluated for injury both visually and using the electrolyte leakage method. The dose response curves from electrolyte leakage data revealed that some species went from no injury to 100% injury over much larger ranges of frost temperatures than other, especially having implications for the accurate quantification of frost resistance of species having injury responses stretched out. Concluded from comparisons of frost resistances found in this study, compared with those found in similar studies, results in this study are believed to be valid and the methods used can be recommended with some modifications. A short time to reach results and good comparability between them are some of the major benefits using artificial freeze testing. Much remains to be discovered regarding frost resistance of New Zealand plants and the mechanisms behind it.

Summering (Swedish summary)

Frosthärdigheten, LT_{50}, bestämdes här för skottstammar och blad hos flera nyzeeländska vedartade växter ur släktena *Olearia* (Asteraceae), *Coprosma* (Rubiaceae) och *Podocarpus* (Podocarpaceae). Det var en del av målen, som inkluderade att försöka hitta potentiellt vinterhärdiga växter för södra kustnära Sverige och lära oss om metoder för köldhärdighetsstudier. Växtmaterialet utsattes för kontrollerade frystester i Sverige sent i november 2006 och i mitten av januari 2007. Växterna hade härdats med svala temperaturer (ca 5-10°C) och naturlig dagslängd. Frosthärdigheten visade sig som väntat vara ganska låg i mycket av det nyzeeländska materialet (ofta mellan –8 och –13°C) jämfört med europeiskt referensmaterial som *Taxus baccata* och *Buxus sempervirens* 'Rotundifolia' (ofta tåligt till lägre än –20°C). Frosthärdigheten som uppmättes i kvistar av *Olearia odorata* var mindre väntad, då den toppade de nyzeeländska arternas frosthärdighet med sina drygt –20°C. Men så har den också växt i tre decennier på Göteborgs botaniska trädgård. Efter den ovanstående rankades de subalpina *Podocarpus* som testades, med stamfrosthärdigheter på mellan –16 och –20°C i januari. De är troligen härdiga i de mildare delarna av södra Sverige, i betydelsen att de överlever där. Generellt behövs det fältobservationer för att kunna fastställa vinterhärdighet. Bladen var generellt sett lika eller sämre frosthärdiga jämfört med stamvävnaderna; hos många arter ökade frosthärdigheten från november till januari; och ett visst samband mellan arternas höjdledes spridning i naturen och deras frosthärdighet kunde ses. Metoden för att testa frosthärdighet var att avklippta skott frystes ned till en serie olika testtemperaturer, varefter uppkomna skador utvärderades dels visuellt och dels genom mätning av elektrolytiskt läckage. Dosresponskurvorna för elektrolytiskt läckage visade bl a att en del arter fick skador tidigt varefter skadorna ökade i ganska jämn takt ned till låga temperaturer. Osäkerheten vad det gäller bestämningen av relevanta frosthärdighetstemperaturer är större för dessa arter än för de vars skador ökade snabbare som svar på lägre temperaturer. Genom jämförelser av frosthärdigheten hos växter som testats här och jämförelser med resultat i liknande studier antas de här uppkomna resultaten vara gällande. Metoderna som här använts kan rekommenderas med vissa modifikationer. Uppenbara fördelar med dem är att resultat nås relativt snabbt och att resultaten går bra att jämföra. Mycket återstår att upptäckas kring nyzeeländska växters frosthärdighet och dess bakomliggande mekanismer.

Introduction

The aims with of this project include determining frost resistance in some New Zealand shrubs through controlled freeze testing. The other part of the project is a literature study assessing whether New Zealand woody plants are suitable for introduction to colder areas like southern Sweden, investigate controlled freeze testing as a method for assessing frost resistance and give a broader overview of how plants survive cold temperatures. Apart from a great personal interest in the New Zealand flora it is well suited for a study like this because of its reputation of being poorly winter hardy, thus becoming more of a challenge. Plants of main focus here are of the genera *Olearia* (Asteraceae), *Coprosma* (Rubiaceae) and *Podocarpus* (Podocarpaceae). Several of the species and hybrids are used for landscape and ornamental purposes in New Zealand, but also in e.g. milder parts of the British Isles. They are all more or less evergreen, except *Olearia odorata* which is deciduous. Shrubs of *Olearia* are often called tree daisies because of their daisy flowers, ray florets generally white. Leaves vary largely in appearance and several species are cherished in mild coastal areas for their resistance to strong salt laden winds. *Coprosma* is related to coffee and one of the main attractions is the fruits, which are small berry-like drupes in a wide range of colours. They are edible too. The interesting filiramulate habit, characterised by small widely spaced leaves and interlacing slender branches, is heavily represented in the genus. *Podocarpus* resemble *Taxus*, but are not poisonous and species here tested are very low growing, suitable for ground cover, containers, or rock gardens. Some recently developed hybrids show a fantastic array of coloured shoots.

The New Zealand climate is maritime with, especially in the southern half of the South Island, rather cool summers which can be unreliable with night frosts occurring even in early summer. They are similar to summers of the Nordic countries and that should make New Zealand plants good candidates for introduction to our horticulture. Many of our already introduced woody plants come from areas of much warmer summers, which gives them a poor development here. The main obstacle of the New Zealand plants is thought to be their winter hardiness (i.e. ability to survive winters), of which frost resistance is an important component. Frost resistance is the ability of plant tissues to cope with and survive temperatures below 0°C. This is possible through strategies of avoidance (i.e. ability of plant tissues to remain unfrozen, keeping water in a fluid state) and freezing tolerance (i.e. ability of

tissues to survive by allowing ice to form extracellularly but not in the protoplast) (Sakai & Larcher, 1987).

Hypotheses to be tested:

- There are New Zealand species or hybrids which can tolerate the winter temperatures of southern coastal Sweden, rendering them potentially winter hardy.
- There is a connection between the plant's frost resistance and smaller leaves.
- There is a connection between the plant's frost resistance and altitudinal distribution.
- The species have a higher frost resistance in January compared to November (Northern Hemisphere), commonly found in other groups of plants.

Frost resistance and winter hardiness

Introduction

Winter hardiness can be defined as the ability of a plant to survive winter (Sakai & Larcher, 1987). The text will deal with this topic only for woody plants, which overwinter with living organs above ground. Some contents will however be of general applicability to plants.

A plant most often surviving winters but frequently getting significant damage could be said to be of poor or limited winter hardiness in this particular area. A plant able to survive winters and reproduce would probably be regarded as satisfactorily hardy. But winter hardiness is a broad term, which includes several variables and stresses the plant will be influenced by (Bärtels & Roloff, 2006). Low temperature is however the main direct or indirect stress factor during winter and, as will be seen, frost resistance largely decides winter hardiness.

Even temperatures above 0°C, but below 10 or 15°C, are harmful to many tropical and subtropical plants. Such plants are referred to as chilling sensitive. Damage is related to membranes in the cells loosing function. Many chilling sensitive plants can however tolerate chilling temperatures provided they are acclimated to cool temperatures, achieved by a gradual decrease in temperature. Another type of damage can occur in these plants at cool temperatures when leaves are exposed to high photon fluxes. This leads to photoinhibition, which damages the photosynthetic apparatus. Frost- or winter desiccation is another problem associated with sunlight and wind, shortly dealt with under “Some more winter problems” (Taiz & Zeiger, 2002).

Frost injuries occur at temperatures below 0°C and are associated with ice formation in the plant. The temperature in plant tissues is generally adjusted to the temperature of the surrounding air very fast. Large succulent plants that are containing a lot of water do however take longer to cool down. Generally the water in the plant will get colder than 0°C when at frost, and the ability of the plant’s different parts to tolerate a certain degree of frost is called their frost resistance, or frost hardiness (Sakai & Larcher, 1987).

Acclimation, hardening, is needed for plants to gain their full inherent frost resistances. This means that the frost resistance in a plant varies with the season, as shown in numerous studies

(e.g. Sutinen *et al*., 1992; Bannister & Polwart, 2001; Lennartsson & Ögren, 2002). It explains why a plant may be damaged by a light frost in summer, but tolerates heavy frosts in winter. The state of acclimation is dependent on both a growth phase factor and an acclimation factor. The growth phase will decide the plants readiness to harden. In many woody plants a prerequisite for them to be responsive to cold acclimation stimuli is that growth has terminated, resulting in dormant buds. As a comparison most herbaceous plants are cold acclimating more simply without a preceding stage of readiness. In these plants the acclimation process is triggered directly as a response to low temperatures (Larcher, 1995). Mechanisms of cold acclimation are discussed further on.

Plants utilise some basic strategies to deal with frost. Such strategies often differ between tissues in the same plant, thus frost resistance often varies largely between tissues. Therefore it is impossible to say that a plant has a certain frost resistance, when in fact it varies between and even within the organs of the same plant (Sakai & Larcher, 1987). The frost resistance of organs like leaf, bud or root is however often generalised as a single temperature.

Roots are less frost resistant than shoots. Colombo (1995) found that frost resistance was greater at the terminal bud and least at the root tips in first-year seedlings of *Picea mariana*, with changes between these extremes along the stem and root being gradual. Immature twig tips are however generally much more frost sensitive than mature stems. The first frost loss in a plant is however often its temporary ability to propagate sexually. Leaves and buds are generally more sensitive than stems. Loss of foliage in evergreen plants is seldom a great problem for the survival, nor is partial damage to the shoot system. If the cambium remains intact or largely undamaged the plant will probably recover. In winter the cambium is often the most frost resistant tissue of the stem in plants from cold climates, while it can be slightly more sensitive than the woody tissues in trees and shrubs from mild winter regions. In the latter stem tissues however often show similar resistances. Woody plants generally die if severe damage occurs at the frost sensitive lower stem and rootstock. But even if woody plants survive after some severe damage, their growth will be reduced for many years (Sakai & Larcher, 1987).

Frost survival strategies

The main frost survival strategies have been termed freezing avoidance and freezing tolerance. Under natural conditions plant cells are killed if ice forms within the protoplast. This is termed intracellular freezing and the growth of ice crystals is believed to mechanically destroy membranes within the cell. Under laboratory conditions plant tissues can be very rapidly frozen, i.e. faster than 10 000 K/minute, to very low temperatures, and survive if thawed at a rapid rate again. Under such conditions water freezes within cells too, but ice crystals are too small to make any significant damage. The avoidance strategy utilises supercooling, which is the cooling of a liquid below its freezing point without freezing taking place. It is termed persistent supercooling when living cells and tissues are able to avoid ice nucleation (i.e. freezing) for long periods. Deep supercooling is the suppression of ice formation at temperatures very far below 0°C, whereby tissues can survive down to ca –40°C. Ice crystals start forming spontaneously at this temperature, and is therefore the limit for supercooling (Sakai & Larcher, 1987).

In freezing tolerant tissues the water on the surface of the cell or between the cell wall and the protoplast freezes, without being damaging. The protoplast is more or less dehydrated by water moving out to the ice. It is termed extracellular freezing and is, according to Sakai & Larcher (1987), more effective in allowing for high frost resistance than supercooling. A prerequisite for it to work is however that the rate of temperature decrease is slow. The degree of resistance to frost in these species is partly dependent on their capacity to accommodate the volume of growing ice crystals, and partly to the ability of the protoplast to tolerate dehydration (Taiz & Zeiger, 2002).

Taschler and Neuner (2004) investigated the summer frost resistance in 33 alpine plant species and found all of them to tolerate extracellular ice formation. In a different study by Lipp *et al*. (1994), frost survival strategies in high-elevation Hawaiian plants were studied. Night frosts are frequent in their environment. They found four out of five species to possess freezing tolerance, with the last relying on persistent supercooling. In leaves of two of the freezing tolerant plants ice formed at around –5°C, but they could tolerate extracellular ice formation down to –15°C and –12°C, respectively. Mucilage seemed to act as an ice nucleator extracellularly in these species. One species tested had a unique freezing pattern in that it supercooled down to –9.3°C, but still tolerated tissue freezing to below –15°C.

Sakai and Larcher, 1987, introduced a third frost survival strategy they called extraorgan freezing. They defined it as “ice segregation from a supercooled organ to a specific space outside, resulting in dehydration of the organ”. It was concluded to be something in-between tolerance and avoidance.

Cold acclimation

Plants need to cold acclimate, cold harden, to tolerate lower temperatures. Xin and Browse (2000) stated acclimation to freezing temperatures to be very complex and to be composed of several interacting pathways. Much remains to be understood. One conclusion they drew was however that the very presence of an acclimation process instead of constitutive tolerance must mean that the biological costs of constitutive tolerance are too high to be selected for in evolution. According to Taiz & Zeiger (2002) more than 100 genes are up regulated by cold stress, though all of them may not be associated with cold tolerance.

A period of shorter photoperiods and cool non-freezing temperatures is known to initiate cold- or winter acclimation in many plants. Additionally, for some plants to reach their highest frost resistance a period of frost temperatures is required (Sakai & Larcher, 1987; Taiz & Zeiger, 2002). The timing and rate of acclimation is of similar or even greater importance than the potential frost resistance, since only present frost resistance counts at the moment frost strikes. Von Fircks (1992) found winter damage in *Salix* to be due to incomplete winter acclimation rather than inability to develop enough tolerance to the temperatures concerned. Bannister and Polwart (2001) investigated frost resistance of ericoid heath plants in the British Isles and found their frost resistance to increase with shorter day length and decrease with higher temperatures. They speculated that global warming might result in increased sensitivity to frost in these species.

In some species a short period of maybe only one or two days warm temperatures may be enough for the plant to loose much of its frost resistance. Phillips & Rix (1994) brougth this topic up when stating that continental species tend to spring out too early in spring in maritime climates. Lennartsson and Ögren (2002) provided an example supporting some differences between maritime and continental plants. They found northern/continental clones of *Salix* were earlier and much faster cold acclimating than southern/maritime clones. The

above discussion partly explains why the right provenance of a species can be crucial for whether it will succeed in a certain climate.

The growing season is also of importance to plants frost resistance. If the species requirements of growing season length, temperatures and other special conditions have been met, and it is healthy, it will be able to cold acclimate deeper than a plant whose requirements have not been fulfilled. One of the components in this context is summer ripening of wood (Sakai & Larcher, 1987).

But what happens in the plant as it is acclimating to cold conditions? Lennartsson and Ögren (2002) found increasing sucrose-to-glucose ratios and especially increasing dry to fresh weight ratios at early cold hardening in *Salix*. Sundblad *et al*. (2001) concluded that stem lignification, dry weight fraction, starch, glucose, fructose, galactose, sucrose, raffinose and stachyose concentrations together explained the majority of the variation in frost hardiness in Scots pine and Norway spruce.

In plants, ice nucleates around e.g. large polysaccharides and proteins, which are called ice nucleators. If the plant survives by extracellular freezing, such molecules are welcome in extracellular spaces, as indicated in a study by Lipp *et al*. (1994). There are also special antifreeze proteins, which can help limit the growth of ice crystals by binding to them. Some sugars and proteins are thought to help to stabilise proteins and membranes during the dehydration, which results from water freezing outside cells or organs. In lowering the freezing point by the presence of solutes, sucrose dominates, but several other sugars can be involved (Taiz & Zeiger, 2002).

It seems like ABA (abscisic acid) is involved in inducing frost resistance, since plants develop some frost resistance at non-acclimating temperatures when treated with ABA. Not all genes involved in cold acclimation are ABA dependent though (Taiz & Zeiger, 2002). Dwyer *et al* (1995) found that an application of paclobutrazol to the New Zealand shrub *Pittosporum eugenioides* increased the foliar frost resistance. Paclobutrazol is a gibberelin biosynthesis inhibitor. The effect was counteracted by application of gibberelic acid.

Some more winter problems

Winter means several problems apart from the effects of ice formation in the tissues. Frost drought or winter desiccation is a problem especially in evergreen plants exposed to sun and wind while the ground or stem is frozen. Leaves are loosing water that cannot be replaced. A second danger is when ice or snow encases plants for long periods leading to high respiratory CO_2 and low O_2 levels. This makes toxic substances accumulate via abnormal metabolic pathways. Heavy snow can inflict mechanical damage. Plants covered in snow for long periods can loose frost resistance, and a constant temperature of 0°C with darkness and high humidity facilitates attack by some fungi (Sakai & Larcher, 1987). Many plants do however rely on snow cover for protection against severe cold and frost drought.

Methods for assessing frost- and winter hardiness

Field trials

Field trials are in wide practice for investigating winter hardiness, i.e. ability to tolerate and survive winter conditions. One of their major benefits is showing whether a plant will be suited for growing in an area, which includes suitable conditions during both winter and growing season. Field trials are needed because no controlled laboratory tests will be able to exactly imitate all the stresses and variables existing in the field. They are however time consuming (Sakai & Larcher, 1987). It will often take many years before anything more certain can be concluded about the plants since all years are different. Only after such long-term experiences plants can be ranked into winter hardiness zones (Bärtels & Roloff, 2006). Metcalf (2000) concluded it in the end to be "a matter of trial and error" to determine if a plant is hardy in a certain area. Testers are often waiting for a "test winter" (Sakai & Larcher, 1987); an unusually tough winter with e.g. prolonged periods of very hard frost, close to cold records, maybe in severe combinations like strong winds and little snow in the autumn or spring. Such an approach may take more than 20 years. Laying trials in areas known to be extra harsh is a way of making the evaluation process more efficient.

Harris *et al*. (2001) provides an example at milder latitudes when populations of *Cordyline australis* from around New Zealand were to be grown in field trials. A field trial in Auckland in the mildest parts of the country turned out to be of little value for evaluation of differences in cold hardiness since no populations were damaged, while many of those in the South Island locations were. A broader spectrum of New Zealand plants have been tested under field conditions for selection of hardy material in e.g. France (Harris *et al*. 2000), and as presented by Söndergaard (1989), in some of the Nordic countries. The measure is generally field survival, which means visually ranking plants to dead or unaffected and a scale in-between for different levels of damage. Having fields at many places increases the chances of selective pressures at some sites, and also gives a broader picture of the plants since other factors like soil and precipitation probably differ. After the winter 1978/79, which was the most severe experienced since 1962/63 in Great Britain, information on winter damage to a large amount of different plants in gardens and parks all over the country was gathered and published (Beckett & Beckett, 1980). One of their greatest difficulties was assessing the different types of weather experienced in different places, and its varying effects on plants. As with field

trials generally exact causes and time of damage were not certain, but certainly differed around the country and made comparability low. A valuable broad picture of winter hardiness in species and cultivars was however supplied.

Controlled freeze tests

Winter hardiness is difficult to test under controlled conditions. But frost resistance, an important part of the former, can be assessed this way. Such standardised tests are useful for quantifying the frost resistance, e.g. for good comparability between genotypes or within the genotype at different stages of acclimation, and for making closer studies on cold resistance mechanisms (Sakai & Larcher, 1987). Several studies have also found results from controlled tests to be in good agreement with field trials, field observations or natural distribution of species (e.g., Sakai & Wardle, 1978, Sakai & Larcher, 1987; Harris & Decourtye, 1995; Bannister, 2003; Taschler & Neuner, 2004). The lack of a common standard in controlled tests results in lower comparability between the work of different researchers.

Controlled tests almost always involve exposing plants, whole or excised parts, to decreasing subzero temperatures landing at some target temperature, which is held for a certain period followed by increasing temperatures. Thereafter injury to frozen plants / tissues is evaluated with one or several of the injury assessment options available. Commonly several target temperatures are tested in order to bracket temperatures leading to no injury, intermediate injury and maximum injury (Ritchie, 1984; Sakai & Larcher, 1987). A dose-response curve may be drawn and the temperature for some critical level of injury, often LT_{50} (lethal temperature for 50% of plants, tissues, cells etc.), used as a measure of frost resistance. The response curve has a sigmoid (S) shape. It can be interpolated to find a critical temperature corresponding to e.g. LT_{50}. A regression using the logistic function is sometimes fitted to the data, although Verwijst & von Fircks (1994) concluded that data often is of asymmetric sigmoidal nature and therefore the Richards function is better to use. Here, the point of inflection between the asymptotes may be used as a measure of frost resistance. Sakai & Wardle (1978) used the point of no or just beginning injury, about LT_0 to LT_{10}, for frost resistance, which would mean their values are under-estimations of frost resistance compared to those from many other authors. To conclude on this issue, injury levels obtained with a certain method will have to be correlated to what happens to the plant in reality to be really informative. The injury level at which the plant can still regain growth is important (Eva

Stattin, pers. comm.). Further, the accuracy of frost resistance estimation might be increased by using two or more methods for assessing injuries simultaneously (Sutinen *et al*., 1992).

Materials used for freeze tests vary as previously mentioned. When possible it is preferable if whole plants are frozen, because this is closer to natural conditions and it is also possible to visually assess plants for re-growth afterwards. Roots are often protected during such tests because they are generally more sensitive and normally protected in the ground. When material is scarce or plants are large it is more practicable to cut out branches or even smaller parts for testing (Sakai & Larcher, 1987). But shrubs and branches of large trees have also been freeze tested *in situ* using special portable freezers (Neuner *et al*., 1997; Taschler & Neuner, 2004). Sakai & Larcher (1987) said experience shows that resistance of excised parts show good agreement with observations made in field after severe frost. Neuner *et al*. (1997) found foliar frost resistance in attached and *in situ* branches of *Nothofagus menziesii* to be on average 1°C better than corresponding branches excised and tested in the laboratory, although admitting some more factors differed.

Conditions plant material has been exposed to before testing will influence its degree of cold acclimation. Some authors expose all material to be tested to a common hardening regime of several weeks in order to overcome some different growing or handling conditions and to induce acclimation close to the maximum potential frost resistance (Sakai & Wardle, 1978; von Fircks, 1992). Freezing rate and thawing rate influence frost resistance and should be standardised. Too fast decrease in temperature is more damaging, as is fast thawing. An unpublished source referenced by Ritchie (1984) claims that cooling rate should not exceed 5°C/h, while thawing may be up to 10-20°C/h. Natural rates of cooling are however probably closer to 1-2°C/h, often used in studies. Sakai & Larcher (1987) called a cooling rate of 5-10°C/h direct cooling, which is used to avoid the material developing greater frost resistance during cooling. They concluded this to be useful for determining the actual level of frost resistance at a given time. Gradual cooling is lowering the temperature stepwise and slowly, allowing the material to develop maximum frost resistance. It has been advised to add ice to material at the initial phase of freezing in order to initiate ice nucleation and prevent supercooling. Just wetting leaf surfaces will have a similar effect, since this water freezes and soon induces freezing inside leaf tissues. Plants or tissues known to survive by avoidance, i.e. not being freezing tolerant should however be allowed to supercool if their supercooling

ability is tested (Sakai & Larcher, 1987). Target temperatures are held for a standard time. According to Sakai & Larcher (1987) four to six hours is a minimum to avoid samples being in a state of supercooling. Also, at temperatures below –30 to –40°C ice formation is very slow. But exposure to target temperatures for 2 h (von Fircks, 1992) and 3 h are also used (Stener *et al*., 2002).

Injury assessment methods

After freeze testing, whole plants may be held in a greenhouse for forcing and later visual assessment of injury and regrowth (Greer *et al*., 1989; Herrick & Perry, 1995). Even excised parts like shoots can be planted as cuttings for forcing and similar assessment of leaf damage, bud burst or rooting (von Fircks, 1992; Stener *et al*., 2002). Another type of visual assessment is placing material in water (Sakai & Wardle, 1978) or polythene bags with damp paper (Bannister & Lee, 1989; Bannister & Polwart, 2001) and, after time required for entire frost damage to show, visual assessment of tissues for browning or blackening e.g. from oxidation of polyphenols (Sakai & Larcher, 1987). Chlorophyll fluorescence (Lennartsson & Ögren, 2002) and digital image analysis are other methods which have been employed for leaves and stems (Neuner & Buchner, 1999). Tissue staining techniques are available for detecting different types of damage (Sakai & Larcher, 1987).

The electrolyte leakage method is a different approach. According to Flint *et al*. (1967) Dexter, Tottingham and Graber first described it in 1930. Damaged cells leak solutes. By placing tissues in water and after some time, often 24 h, measuring electric conductivity of elute a quantification of damage can be achieved. Electrolytes released are proportional to electric conductivity of elute. It has been widely employed (Sutinen *et al*., 1992; *Colombo et al*., 1995; Neuner & Buchner, 1999; Sundblad et al., 2001; Lennartsson & Ögren, 2002; Stener *et al*., 2002; Eva Stattin pers. comm.). In 1967 Flint *et al*. presented a method for expressing freezing injury by converting percentage release of electrolytes to a scale where the unfrozen sample, although leaking some solutes, was given a value of zero and the heat-killed sample a value of 100. The percentage release from each sample was calculated as a relation between the release before and after heat killing. They called it Index of Injury. Some certain Index of Injury could be used as a measure of frost resistance. It has however often been discovered totally frost damaged tissues are not leaching as much as after heat killing, and this maximum Index of Injury below 100 varies between different species and tissues.

One solution could be to make a frost killing of all tissues instead of heat killing for more accurate reference values (e.g. Lennartsson & Ögren, 2002). Or the relative conductivity values obtained with heat killing are used, with the maximum and minimum relative conductivity (after hard freezing and no freezing, respectively) for each species or tissue put to 100 and 0, and 50 is used for frost resistance (Sutinen *et al*., 1992). Anyhow data can be fitted to the logistic function or even better to Richards function (Verwijst & von Fircks, 1992). Ritchie (1984) discussed electrical impedance of tissues as an alternative less time and labour consuming method, although less accurate too.

Some other methods employed in frost resistance research

Exotherm analysis is a way of determining when water freezes in the tissues. As it does, energy is released and can be detected as a temperature increase by thermometers attached to plant tissues during freezing. Tissues or organs relying on supercooling for frost resistance are killed when this water is freezing (Sakai & Larcher, 1987).

There is a search for less labour- and time-consuming methods for large-scale assessment of frost resistance in plants. Lennartsson & Ögren (2002) found the NIR (near infrared) spectroscopy preliminary promising for screening in *Salix*. Using the visible plus near infrared (VIS + NIR) spectra of shoots of conifer seedlings has been found to be a reliable estimator of frost resistance. It is based on causal relationship between spectra and physiology of plant frost hardiness. No freezing is needed and plant material is not damaged (Sundblad *et al*., 2001).

Methods used in this study

These are just some concluding remarks on which methods were used here and why. For more details see Materials and Methods. As the time for this project was limited there was a need for quick results. These could not be provided by field trials, so artificial freezing was employed. Plant material was also limited and thus testing of excised shoots was an attractive option to increase sample number and allow for individual scatter. As indicated before, results from controlled freeze tests have been agreeing closely with field observations (survival) in several studies, although differences are to be expected since conditions are never completely simulated in artificial tests (Sakai & Larcher, 1987). Winter hardiness was not determined in

this study, while frost resistance at two points in time for leaves and outer stems were. Two great advantages using this type of method, apart from time savings, are the quantitative data on frost resistances and the possibility of comparing these between different tissues, different plants, and different times of the year. Sakai & Larcher (1987) concluded artificial freeze tests to be required for physiological studies of frost resistance mechanisms, including the annual pattern of variability in resistance and the potential frost resistance at different stages of growth and maturity. This powerful tool was not nearly fully utilised in this study, but was more used as a screening of resistance levels in a rather large plant material.

In order to get quantitative data of frost resistances, two injury assessment options were chosen: visual damage assessment and electrolyte leakage assessment. This combination was used by Stener *et al*. (2002). They found the electrolyte leakage to be the most reliable estimator of frost resistance compared to the visual damage and dry weight to fresh weight fraction in beech (*Fagus sylvatica*) shoots. As indicated in the text about injury assessment methods the electrolyte leakage method is widely used and generally found reliable. Ritchie (1984) concluded it to be so, but having drawbacks of being a bit laborious and creating problems of predicting the critical level of electrolyte leakage that corresponds to plant- or organ death. Much of the work done on frost resistance of New Zealand plants has however not utilised the electrolyte leakage method, but rather visual injury assessment (e.g., Sakai & Wardle, 1978; Bannister & Lee, 1989; Greer *et al*., 1989; Bannister *et al*., 1995; Neuner & Bannister, 1995; Neuner *et al*., 1997; Darrow *et al*., 2001). Visual injury assessment can thus be seen as necessary to allow for reasonable comparisons. Reitsma (1994) did however use the electrolyte leakage method for some New Zealand plants. Finally, to decide frost resistances from injury data linear interpolation was the main method used, although logistic regression was tried too. LT_{50} was used as the measure of frost resistance. It has been commonly used in numerous studies, although unfortunately not by Sakai & Wardle (1978), who rather decided the lowest temperature where no or very little injury occurred. Bannister (2003) did however conclude frost resistance temperatures determined for a particular species by different authors using different methods for either the determination or the expression of it often show considerable overlap.

Climate and geography

Frost

Frost is defined as environmental temperatures below 0°C. Both cold and frost are important factors limiting where plants can grow, as discussed in the section about cold stress tolerance. Only 25% of the world land area can be considered absolutely frost free, and 48% of the land has a minimum air temperature below –10°C. Lower temperatures are encountered at higher latitudes, higher altitudes, and with increasing distance from the sea (Sakai & Larcher, 1987).

Frosts are subdivided into advective and radiational, with the former occurring when a generally large body of cold air is moving in from a distant area. Typical radiational frosts happen on clear and often calm nights with a large loss of heat to the atmosphere. A combination of them can result in very low temperatures. Meteorological measurements are generally made 2 m above ground (Sakai & Larcher, 1987). On a cold night the air layers near the ground or plant stand surface are 2-5°C cooler than the air at 2 m above the ground. Consequently, extreme temperatures recorded at the normal level are likely to be even lower closer to the ground. In dense vegetation the coldest will be at or just below the exposed surface of the plants, while temperatures will not drop as far further into the vegetation (Sakai & Larcher, 1987).

On still clear nights the cold air tends to flow down hills and collect in depressions and valley floors with restricted air drainage, which can result in such places becoming 8°C colder than the surrounding higher ground. This temperature inversion leads to pronounced effects on the flora in inland sites of New Zealand, where the more frost sensitive species might be growing on the slopes above the more cold tolerant species growing on the valley floor (Wardle, 1991).

Climate and geography of New Zealand and Sweden

Mainland New Zealand has three islands: North Island, South Island, and south of South Island the smaller Stewart Island. With some adjacent smaller islands they cover over 263 000 km² and extend between latitudes 34°S and 47°S (Wardle, 1991), which can be compared with ca 55°N to 69°N for Sweden. The closest large landmass is Australia, 1800 km to the west. Nowhere in New Zealand is more than 130 km from the sea (Metcalf, 2006), meaning it

has a very maritime climate. There are several groups of smaller islands far out from the mainland, including the Chatham Islands to the east. They are truly oceanic (Wardle, 1991). Looking for plants hardy in northern Europe might seem like a wasted effort, but there are some encouraging circumstances in addition to the wisdom that nothing is known until it has been tested.

Climatic contrasts in New Zealand are sharpest from the west to east due to a mountain chain extending most of the length of the country, with many peaks over 2000 m in the Southern Alps of the South Island. Here is also the highest mountain of over 3700m, Mt Cook. In the central parts of the North Island is a central plateau with active volcanoes. Westerly winds dominate and a succession of anticyclones is moving to the east. Between these come depressions with rain giving very high precipitation in the mountains to the west. The mean annual rainfall ranges from 8000 mm on the western side of the Southern Alps to 300 mm in a small area of Central Otago, an area east of the Southern Alps in the southern part of the island. Most parts of New Zealand have annual rainfalls of 600-1500 mm (MetService NZ, 2007). This can be compared to the usually 500-750 mm of southern Sweden (see table 1).

Mean annual air temperature at sea level decreases from ca 15°C in the far north to about 10°C in the southernmost parts. July is the coldest month, corresponding to January in Sweden, while January and February are the warmest (MetService NZ, 2007). See table 1 to realise the mean temperatures in summer are very similar between Sweden and the South Island. The annual sunshine hours range from 1600 in Southland (southernmost South Island) to 2000 in the main part of the country and some places exceeding 2400 h.

The annual range of mean temperatures can be used as a measure of how mild the climate is. For the mildest western and northern parts the range is 8°C and it reaches a maximum of 14°C in Central Otago, which has an approach to continental climate (MetService NZ, 2007). From table 1 it can be concluded that the annual range of mean temperatures in southern Sweden exceeds this by at least 2°C, indicating even the mildest parts of Sweden has a more continental climate in this respect. Using the extreme temperature range, from lowest and highest temperature ever recorded, Ophir in Central Otago with 55°C (MetService NZ, 2007) exceeds the Swedish Falsterbo by almost 5°C. Falsterbo is situated out on a small peninsula in southernmost Sweden.

The coldest winter temperatures in New Zealand are experienced in Central Otago, the MacKenzie Plains of inland Canterbury, and on the central plateau of the North Island. The cold record of –21.6°C was measured at Ophir in Central Otago, but generally night temperatures as low as –12°C are rarely recorded even in these areas. Elsewhere winters are milder, with the extremes of a frost free coastal stretch in the northernmost North Island. The snow line is about 2000 m in the Southern Alps in summer. In winter snow may stay for a few days in the lowlands on the east coast of the South Island. Inland snow is more frequent, but generally not persistent below 1000 m (MetService NZ, 2007).

The intensity and length of the frost period is the main difference between New Zealand and northern European winters (Colin Meurk, pers. comm.). Temperatures rarely stay below 0°C for several days, but frosts may come even in the summer.

The Swedish climate is favourable considering its latitudinal position similar to Alaska and Siberia. The Scandinavian Peninsula is surrounded by sea and is positively influenced by the Gulf Stream. The climate of the milder parts of the most southern province of Sweden, Scania, is similar to that of Denmark and northern Germany with little snow cover. Southern coastal Sweden has a strong maritime influence, but the high latitudes and close proximity to the continent does however give cold winters some years. The northern provinces of Sweden are strongly influenced by the eastern continental climate in the winter when the Gulf of Bothnia is covered with ice (Ullström, 1966).

Table 1. Climate data for southern Sweden and the South Island of New Zealand. (Swedish data: SMHI, 2006. New Zealand data: MetService NZ, 2007). Years in table not relevant for NZ data. They are instead: 1969-1998 for rainfall and sunshine hours. 1961-1998 for mean annual-, mean July- and mean January temperatures. And full historical record for temperature extremes.

	Mean annu. temp. 61-90	July mean daily temp. 61-90	January mean daily temp. 61-90	Extr. Max temp. Since 1901	Extreme Min temp. Since 1901	Mean annual precip. (mm) 61-90	Mean annual sunshine hrs 61-90	Mean annual extreme low temp. 1992-2006	"USDA zone" (92-06)	"USDA mid-Europe zone" (92-06)	Swed. Zone
Falsterbo	8.0	16.4	0.3	30.2	-20.2[1987]	491		-9.0	8	8b	1
Malmö	7.8	16.5	-0.7	34.0	-28.0[1942]	602		-13.9	7	7b	1
Lund	7.9	16.8	-0.6	33.9	-26.3[1942]	666	1592	-14.5	7	7b	1
Helsingborg	7.6	16.1	-0.9			737		-14.4	7	7b	1
Kristianstad*	7.0	16.1	-1.3	33.6	-27.8	562		-17.2	7	7a	1
Visby airport	6.6	16.0	-1.3	32.0	-25.4[1966]	513	1882	-14.7	7	7b	1
Växjö	6.3	15.8	-2.7	34.4	-34.0[1942]	653	1440	-19.0	6	6b	3
Kalmar airport*	6.8	16.4	-1.9	35.2	-31.0[1942]	484		-19.5	6	6b	1-2
Varberg	7.3	16.2	-1.3	32.5	-25.5[1942]	738		-14.9	7	7b	1
Göteborg	7.7	17.0	-1.1	33.8	-26.0[1942]	758	1722	-14.9	7	7b	2
Stockholm	6.6	17.2	-2.8	35.4	-28.2[1942]	539	1821	-14.4	7	7b	2
Hokitika[WC]	11.7	7.4	15.5	29.7	-3.2	2865	1850		9		
Christchurch[EC]	12.1	6.5	17.4	41.6	-7.1	635	2035		9		
Lake Tekapo[C]	8.9	1.7	15.2	33.3	-15.6	604	2206		8?		
Alexandra[CO]	10.8	3.1	17.1	37.2	-11.7	356	2042		8		

*Some of the annually lowest temperatures used for the calculation of mean annual lowest temperature for the last 15 years have been recorded on a location nearby the location stated.
The New Zealand places are all in the South Island: WC = West Coast. EC = East Coast. C = inland Canterbury. CO = Central Otago.

Plant hardiness zones

New Zealand's climates have been described as subtropical in the far north, warm-temperate over much of the country and temperate in the far south (Metcalf, 2006). Today it is however common to divide climates and woody plants into winter hardiness zones based on the USDA zones. The USDA map for North America was developed by the United States Department of Agriculture in 1960, and reworked and printed again in 1965 and 1972. It is a system for trees and shrubs and is based on the mean annual minimum temperature measured 2 m above ground. Heinze and Schreiber translated these zones to European conditions in 1984. They further subdivided zones 5-8 into a and b to make the Central European map more precise (Bärtels and Roloff, 2006). See table 2 for the limits of the zones and some indicator plants.

A world map with USDA zones can be seen in Cheers, 1999. At this scale it is inexact, but following it New Zealand has zones 7-11. Zone 7 is only in a smaller area of the Southern

Alps. Zones 10-11 are in the upper part of the North Island. Interior parts of the islands are zone 8, while the rest is zone 9.

According to the European zone map based on USDA zones in Bärtels and Roloff (2006) southern Sweden is zone 7, which seems partly but not entirely correct as seen from table 1, with e.g. Växjö in the inland probably being zone 6. The USDA zones given for Swedish places in table 1 are only calculated for mean annual minimum temperatures of the last 15 years. South-western coastal Norway is zone 8, as is parts of coastal Denmark with Bornholm. Coastal Sjaeland is 8a, and inner parts 7b. There is even one part of southern Denmark given zone 8b. A map of the USDA zones for the British Isles in Chalk, 1988, reveals the coastal parts of Britain and Ireland are zone 9, with inner parts zone 8, and parts of the inner Scottish Highlands zone 7.

Table 2. USDA zones based on mean annual minimum temperatures. (°C, 2 m above ground). With some indicator plants which grow in respective zones but not in lower zones. From Bärtels and Roloff (2006).

Z5	-28.8 to -23.4	*Acer campestre, Cornus mas, Taxus cuspidata*
Z6	-23.3 to -17.8	*Buxus sempervirens, Hedera helix, Taxus baccata*
Z7	-17.7 to -12.3	*Ilex aquifolium, Prunus laurocerasus*
Z8	-12.2 to -6.7	*Araucaria araucana, Magnolia grandiflora*
Z9	-6.6 to -1.2	*Citrus spp., Laurus nobilis, Olea europaea*
Z10	-1.1 to 4.4	*Annona cherimola, Musa basjoo*
Z11	>+4.4	*Cocos nucifera, Theobroma cacao*

It is worth mentioning the USDA zones fail to take notice of the variation and duration of winter and summer temperatures, and most other factors of importance to plants survival and growth. Or, as Chalk (1988) stated, zone hardiness figures can only be a guide.

Sweden has another zone map, however mainly useful within the country. A first step towards it was published in 1910 by a Swedish fruit society (*Sveriges pomologiska förening*). It was originally based on February isotherms and comprised four zones. It has since been redeveloped several times, and now contains eight zones, with zone one being the mildest. Zone eight is bordering onto the Swedish alpine regions. These zones are largely based on practical growing experiences with trees and shrubs, and with different fruit tree cultivars in particular (Ullström, 1966). This zone system is the one primary used for garden trees and shrubs within Sweden.

New Zealand has the LENZ system (Land Environments of New Zealand). It is a classification of New Zealand's land environments and was provided by Landcare Reasearch and the Ministry for the Environment. It is based on a combination of climate, landform and soils data to group ecosystems of similar type (Ministry for the Environment, 2003). It could be used for identifying climatic surfaces of relevance for finding hardy plants (Colin Meurk, pers. comm.).

New Zealand flora

Islands far out from all large land masses are likely to have large elements of the flora endemic, i.e. not to be found anywhere else. This is true in New Zealand with ca 85% of its vascular plant species endemic, although no families are endemic (Wardle, 1991). With ca 2200 species of native flowering plants and almost 200 species of fern the area is not rich by tropical standards or compared to Australia (Spellerberg & Given, 2004), but it is truly unique.

Special features of the New Zealand flora include the high degree of woody plants. Most species are perennial and evergreen, with almost no annual or biennial natives. Some deciduous plants exist (Edwards & Given, 2004). There is a high proportion of white flowers although overseas relatives are often brightly coloured (Spellerberg *et al*., 2004). A high proportion, 12%, of flowering plants are dioecious, i.e. have male and female flowers on separate plants (Edwards & Given, 2004). *Coprosma* and *Podocarpus*, which are dealt with more in this report, are examples of the latter.

There is a common shrubby habit in many New Zealand plants. Wardle (1991) proposed it to be called a filiramulate habit (see figure 1; A and C) Some of its common characteristics are slender, interlacing twigs with small leaves placed distantly or in distant clusters. They are commonly called divaricating shrubs, although not all have the wide-angled branches this actually refers to. Many different families and genera have filiramulate representatives in the country. Why is this habit so common in this country? One theory says it has evolved as a defence against the large now extinct moa birds, which were browsers. Another believes it to be an adaptation to harsher climate.

Wardle (1991) says lowland forests in New Zealand are similar to those of New Guinea highlands. They contain conifers with succulent fruits (Podocarpaceae), evergreen broad leaved trees, epiphytes, lianes, and tree ferns. New Zealand has 8 species of tall tree ferns and 20 species of conifer, the majority of the latter belonging to Podocarpaceae. These countries are far apart today but once belonged to the super continent Gondwanaland. And so did Chile. The large stands of small-leaved evergreen *Nothofagus* growing in cooler districts of New Zealand resemble those in temperate Chile. In drier districts and at higher altitudes evergreen

tussock grasses may dominate the vegetation, which resembles that of tropical high mountains rather than northern temperate grasslands (Wardle, 1991).

Figure 1. NZ flora. A. *Corokia cotoneaster* showing filiramulate habit. B. Stem of *Podocarpus totara* in lowland forest of the South Island. C. *Myrsine divaricata* showing filiramulate habit in Christchurch botanic garden. D. Lush rainforest with tree ferns on the South Island westcoast. E. Subalpine vegetation by Kepler track in Fiordland Ntl Prk of the South Island. Photos by author.

Trying to understand the distribution of plants today the dramatic history of New Zealand may help. In extreme summary it belonged to Gondwanaland and became isolated about 60-80 million years ago as it separated from Australia. Somewhere in this early history there was uplift of land too, but this ceased and about 24-34 million year ago New Zealand was reduced

to small and warm low-lying islands. In the last 5 million years there has been renewed tectonic activity resulting in increased land areas and high mountain chains. During these last few million years the uplift has been combined with ice ages and volcanism. The last glaciation was from 120 000 to 10 000 years ago. There was not much forest left in the South Island during this time but it more or less quickly spread over these areas again from the north and some remaining pockets. The first humans to arrive were the Polynesians ca 1000 years ago (Wardle, 1991). The first European to come here was Abel Tasman in 1642, but it lasted until 1769 for the next European ship to arrive. This time it was Captain James Cook, accompanied by the botanists Joseph Banks and Daniel Solander who recorded plants where they landed (Chalk, 1988). Europeans began colonisation in the early nineteenth century. Humans, especially the Europeans, changed much of the vegetation. It was largely replaced by introduced species. They also introduced many animals, birds and insects, proving very damaging to native flora and fauna. Some features of the isolation before the arrival of humans was that it had many species of e.g. beetles and moths, but few butterflies and no social long-tongued bees. On land two species of bats were the only mammals apart from seals. There were numerous flightless birds, like the kiwi birds and the 1-3 m tall moa birds (Wardle, 1991). This must have affected the evolution of plants.

There are centres of plant species richness in northern, central, and southern New Zealand, separated by gaps with relative poverty in species. Wardle (1988) conclude the last glaciation is likely to have caused more extinction in the gaps than by the centres. Heads & Craw (2004) defend the New Zealand Alpine Fault biogeographic hypothesis. It proposes the disjunction of species has arisen because they have been pulled apart. The Nelson and Westland provinces have moved north east relative to the rest of the South Island.

Mentioning some of the plants, *Hebe* easily comes to mind since it is the largest genus of flowering plants here. They comprise over 100 species and subspecies, and the absolute majority of them are endemic to the New Zealand botanical region (Metcalf, 2006). They grow from seashore to 2700 m above sea level (Chalk, 1988). Many of them are abundant flowering, have attractive foliage, and are easily propagated (Hobbs, 1994). *Hebe* was formerly included in the Scrophulariaceae family, but is now apparently suggested to be part of Plantaginaceae (Metcalf, 2006). More examples of genera with several diverse woody species dominating many New Zealand landscapes, along with *Hebe*, are *Coprosma* (Rubiaceae), *Dracophyllum* (Epacridaceae) and *Olearia* (Asteraceae) (Heads, 1996).

Tolerance and use of New Zealand flora overseas

General notices on frost resistance of New Zealand plants

The distribution of plants within New Zealand can be used as a guide for finding more cold tolerant species or provenances. Such gradients can be seen with a more southern latitude, higher altitude, and further inland (Sakai & Wardle, 1978; Hawkins *et al*., 1991; Decourtye & Harris, 1992; Harris *et al*., 2001). Nothing is however sure until it has been tested and there are several exceptions. The climate in some mountains can be rather mild with a breeze more or less constantly present. The giant kauri tree, *Agathis australis*, and the spectacularly flowering kaka beak, *Clianthus puniceus*, which are naturally distributed only in the northern North Island but are planted and grown around the coastal South Island (Metcalf, 2000), provide some of the exceptions to the gradients rule.

By Northern Hemisphere standards the New Zealand flora has been found to be relatively intolerant to low temperatures. It is not surprising considering the climate being fairly mild surrounded by ocean and far from large landmasses (Sakai & Wardle, 1978). The high mountains are not that old either, once rising from isolated low lying islands with much more favourable climate (Wardle, 1991). Leaves of the least hardy broad leaved species are not tolerant at –4°C, while the tolerance extends to –18°C to –25°C for the hardiest high altitude conifers. The hardiest New Zealand trees and shrubs compare only with trees growing in temperate lowland Japan. *Cryptomeria japonica* is comparable in hardiness to the hardiest New Zealand conifers, which include *Halocarpus bidwillii*, *Phyllocladus alpinus* and *Podocarpus nivalis* (Sakai & Wardle, 1978). Colin Meurk (pers. comm.) said the flora is generally not tolerant of deep or prolonged frost, but can tolerate light frost during most of the year. Late spring frosts are common even in the coastal parts of the North Island.

Hebe, considered to be a genus with some of the hardier New Zealand plants, is often damaged by frost in the Northern Hemisphere. A typical sign of frost damage in *Hebe* is when the bark of the stem splits open and exposes underlying wood (Metcalf, 2006). Frost damage is mainly confined to the effect of freezing of the cell sap of semi-mature stems (Martin Searle, pers. comm.). He put forward a theory that hebes exposed to hard salt laden winds by the coast are less prone to frost damage since their cell water content is lowered, as opposed to those standing in sheltered situations. Many New Zealand plants are highly appreciated in

the UK and other places, as they seem remarkably unaffected by or tolerant to hard salt laden winds, and they are actually used for shelter in such coastal areas (Ben Rushbrooke, pers. comm.). Shelter from dry and cold winds is however essential for the survival of many temperate evergreens from New Zealand (Phillips & Rix, 1994).

Cold tolerance mechanisms in New Zealand plants

Some New Zealand plants were found to reach their maximum frost resistance in late winter (Neuner & Bannister, 1995). The foliar frost resistance in four species of New Zealand *Pittosporum* growing in Dunedin and naturally hardened increased from –6 to –8°C in March and April to –9 to –10°C in July (Bannister *et al*., 1995). The latter month would correspond to January in the Northern Hemisphere. Generally, woody evergreen plants from regions with very mild winters temporarily arrest growth during the coldest period. Acclimation in many such plants seems to begin suddenly in response to cool temperatures and be completed in just a few days. Many Southern Hemisphere plants, like *Eucalyptus*, have been found to be insensitive to photoperiod with respect to cold acclimation, although subalpine and cool-temperate *Nothofagus* species respond to shorter days (Sakai & Larcher, 1987). The strategy of frost resistance in many New Zealand species is probably frost avoidance by supercooling. Though some studies have shown *Nothofagus* species survive by extracellular freezing tolerance (Neuner & Bannister, 1995). Sakai & Wardle (1978) generally found species frost resistance of leaves to be similar to the pattern in buds and twigs. Coming to the question of the filiramulate habit common in many New Zealand plants, frost resistance of heteroblastic trees was investigated by Darrow *et al*. (2001). The heteroblastic trees have juvenile forms with a filiramulate habit, which is very different from the adult forms. They concluded these juvenile forms were generally not more frost resistant than their mature forms, and that this habit had not evolved to make juveniles more frost resistant.

Warwick Harris (pers. comm.) speculated that the red leaf colouration common in many New Zealand plants is strengthened by exposure to low temperature and high light, and these pigments might act as a sunscreen reducing light damage to chloroplasts in cold or frozen plant tissues. It means the pigments should protect against photoinhibition. Larcher (1995) wrote that anthocyanins are acting as a darkening filter protecting against harmful levels of light. They are particularly common in the unfolding leaves of tropical plants. Furthermore, the quantity of the pigments carotene and lutein is known to increase in chloroplasts as a

response to strong light. The phenomenon might be compared to Northern Hemisphere species like *Thuja occidentalis* and *Cryptomeria japonica* often exhibiting colour changes in winter.

Exotic ornamental plants – New Zealand flora in the world

When discussing moving plants to other places of the country or the world it can be questioned. Why do we want to move plants? Our civilisation is built up by agriculture, horticulture and forestry. Plants used for producing food and other useful products are widely accepted because they are essential for our existence, although they are often grown far away from where they were found in the wild and often replacing large areas of native vegetation. New Zealand has put up very rigid rules against introducing living organisms like plants since they have bad experiences from it. About half of the vascular plant species growing wild in New Zealand are introduced exotic plants which have naturalised. The numbers are increasing every year. A proportion of these plants is termed invasive weeds. They are very competitive in New Zealand and threaten the long-term survival of native species and natural communities. Over 70% of the now invasive weeds were introduced to New Zealand as ornamental plants. The New Zealand Department of Conservation is trying to control the invasive weeds in the natural areas of its responsibility, which is ca 30% of the New Zealand land area (Department of Conservation, 2000).

The situation is however quite different in northern Europe and woody plants native to New Zealand, if surviving winters at all, are not likely to be competitive against the native flora in Sweden due to lower frost resistances. This said, if wanting to introduce plants for ornamental purposes to Sweden it might even be wise looking for tender plants. It is however hard to give many examples of woody plants used for ornamental purposes in Sweden that are naturalising at rates threatening the native ecosystems on land. Peter Bannister (pers. comm.) did however mention New Zealand shrubs like *Griselinia littoralis* and *Pittosporum tenuifolium* have naturalised in southern England. The planting for ornamental purposes is most often done in populated areas where native vegetation was cleared long ago for agriculture or towns and cities. Native plants are also used in such plantings.

The main reasons for moving New Zealand plants would be because they add ornamental values and in some cases are very well suited for growing in a particular situation. These

values can be utilised indoors or out in gardens and parks if they survive winters or are protected during winter. Denmark grows and exports many millions of pot grown *Hebe* to the European market for use as outdoor or indoor pot plants, bedding plants or for decorating graves (Noack Kristensen, 1989; Hobbs 1994). Many of the native plants are now used in New Zealand gardens, parks and restoration projects, where it has become a trend to use native plants. The New Zealand flora was long seen as dull in its home country, with so many evergreen species and maybe not as amazing flowers as some exotics (Spellerberg & Given, 2004).

England and the UK were among the first to appreciate the New Zealand flora for use overseas and today grow many of the New Zealand genera (Edwards & Given, 2004). Some selection and breeding work has been done here, lately by Graham Hutchins of County Park Nursery in Essex (Metcalf, 2006). In the 1980's, Mr Decourtye of France initiated selection for ornamental and cold hardy species from a large number of New Zealand genera (Decourtye & Harris, 1992; Harris & Decourtye, 1995; Harris *et al*., 2000). Some breeding of *Leptospermum* has been done in California (Edwards & Given, 2004), and *Hebe* has been bred some different places but not properly structured in New Zealand until Mr Hobbs (1994) started a program in Auckland lasting the 1980's and 1990's (Metcalf, 2006). Now there is breeding done with several genera in New Zealand (e.g., by Warwick Harris, pers. comm.) and this is likely to increase in the future (Edwards & Given, 2004).

Cordyline (cabbage trees), *Phormium* (NZ flax), *Dicksonia* (tree ferns) and *Pittosporum* are just some of the more popular New Zealand plants grown in the UK and Ireland. *Hebe* is widespread here and appreciated for nice looking foliage and flowers attracting butterflies (Hayter, 2006). The genera of main focus in this report are all well represented in these isles, as seen from the number of nurseries and suppliers selling them (Lord *et al*., 2006). Plants like *Olearia x macrodonta*, *Griselinia littoralis*, *Hebe* and *Brachyglottis rotundifolia* make up the backbone of the gardens of Northwest Highlands of Scotland (ca 58°N). Conditions here are very windy and rainy, and winters are mild with temperatures rarely dropping below –5°C (Ben Rushbrooke, pers. comm.). The Logan Botanic Garden, situated in south western Scotland, is growing a large number of different New Zealand plants successfully. In the last 33 years they have experienced a couple of severe winters. In those winters temperatures have fallen to –10°C and many plants were killed, but still many have survived too (Barry Unwin,

pers. comm.). Spellerberg & Given (2004) gave an example of Portugal growing tree ferns, cabbage trees and so on, and of course many places with winters this warm are able to grow these plants. Harris *et al*. (2000) concluded most of the New Zealand species tested in France to be hardy in the mildest western and southern coastal regions of Europe, not including the inland of France. But they can be restricted by factors like low precipitation or hot summer temperatures too. *Hebe* can only be really successfully grown in a western part of North America, i.e. west of the Cascade or Sierra Nevada Mountains in the Pacific Northwest and California. Most of the remaining parts of North America are either too cold or too hot or both. Some enthusiasts have however been successful with certain species around the Great Lakes and the coastal areas of Newfoundland (Bell & Sauceda, 2006).

Some of the more promising cold tolerant species found in the evaluations in France (Harris & Decourtye, 1995; Harris *et al*., 2000) are *Coprosma propinqua, Corokia cotoneaster, Melicytus alpinus, Phormium cookianum, Plagianthus divaricatus, Discaria toumatou,* and *Podocarpus nivalis*. The *Plagianthus* belonged to the surprises since it is growing in coastal, often saline swamps in New Zealand. Variation in cold hardiness was discovered in several species bearing promise for improvements of cultivars. Selections from these trials have potential to provide ornamentals and amenity plants for a greater area of Europe. However, most of the *Olearia* species tried suffered badly in winters and soon died (Harris *et al*., 2000). Learning from another introduction of New Zealand plants to Europe, this time to Bergen (Norway), the Faroe Islands, and Copenhagen (Denmark), the New Zealand plants survived much better on the Faroe Islands compared to the other two places. This is simply explained by the milder winters and shorter periods of continuous frost. Copenhagen gets the worst winters of these places. *Podocarpus nivalis* and some hybrid were the best performers here, still getting some damage to outer shoots in the coldest winters. *Hebe odora* was another survivor, along with *Hoheria glabrata* and *Hoheria lyallii* which were cut to the ground in severe winters but regenerated from the base (Söndergaard, 1989).

Poland had the most severe winter since 1928/29 in 2005/06. There were frost temperatures for three months and temperature fell to –34°C, with only a thin layer of snow to protect the plants. Just about the only *Hebe* not to be killed to the ground was *Hebe ochracea*. Other survivors more or less damaged were *Hebe pinguifolia* 'Pagei', *H. odora* and *H. rakaiensis* (Grzywaczyk, 2006). Peter Korn (pers. comm.) has tried growing many New Zealand plants outdoors inland from Gothenburg in Sweden. According to him some of them are hardy to –

30°C under good growing conditions. Plants grown by him include *Hebe*, *Podocarpus*, *Phyllocladus*, *Pimelea*, *Melicytus*, *Pittosporum*, *Carmichaelia*, *Corokia*, *Coprosma*, *Leucopogon* and a long list more, and indicate there is more to be discovered in cold hardiness of plants from down under.

Materials and Methods

Plant material descriptions

Coprosma, *Olearia* and *Podocarpus* have been the main focus for controlled frost hardiness testing in this study. Genera and material investigated are here shortly presented, including brief descriptions of reference material. See figure 2 for photos of some of the species tested.

Coprosma

Coprosma, belonging to the Rubiaceae family together with e.g. *Coffea*, has about 90 species in Australasia, with several species located on the pacific islands, e.g. Hawaii. About half of the total species are from New Zealand. They are mainly dioecious and have small inconspicuous flowers. Wind pollinated. Fruit can be showy and is a two- or four-seeded drupe often translucent and coloured e.g. red, yellow, blue, sea green, pink or white. All are edible and roasted seeds are supposed to be a good coffee substitute (Hutchins, 1995). *Coprosma* occupy a wide range of habitats in New Zealand and have significant ornamental interest (Warwick Harris, pers. comm.). There has been frequent natural hybridisation within the genus in New Zealand, concluded from DNA analysis (Wichman *et al*., 2002). With several newly developed cultivars it is one of the best groups of foliage plants within the country, easily propagated from cuttings or seed (Given & Edwards, 2004). A range of frost resistances in the autumn (–8 to –14°C) was determined for leaves from a number of species in the South Island (Bannister & Lee, 1989). Sakai & Wardle (1978) determined frost resistance in the large leaved species *Coprosma lucida* to be –8°C for leaf, bud and cortex, however methods differed between Sakai & Wardle and Bannister & Lee. The four species here tested are small-leaved. All plants except *Coprosma petriei* used for testing came from Graham Hutchins of County Park Nursery in England, August 2006.

Coprosma acerosa var. *brunnea* ‘Blue Beauty’ syn. *Coprosma brunnea* ‘Blue Beauty’
The species is hardy in zone 8-10 according to Cheers (1999). Leaves are 4-16 mm long and narrow-linear, on a prostrate or sprawling plant. The species *C. acerosa*, in which *C. brunnea* is included, grows throughout New Zealand from lowland to subalpine (Poole & Adams, 1994). ‘Blue Beauty’ is a cultivar from Graham Hutchins collected on the west coast of the

South Island. It is a female plant with bright blue fruits. The fruit often last from the summer well into winter. It can hybridise with *C. petriei* (Hutchins, 1995).

Coprosma dumosa

Compact shrub to 3 m tall. Densely leafy and divaricate. Leaves ovate to broad elliptic varying in size around 5 x 2.5 mm, dark green when young and getting lemon yellow when old. Unisexual. Drupe sometimes opaque white but often orange maturing to red, 5-7 mm in diameter. It is distribution in most of the South Island east of the Main Divide of the Southern Alps. It was in 1906 described under the name *C. parviflora* var. *dumosa* by Cheeseman. G.T. Jane recently gave it species status (Jane, 2005).

Coprosma petriei

A prostrate plant with shoots creeping and rooting. Leaves ca 3 x 1-3 mm with tiny hairs. Fruits white, blue or sea green 6-10 mm (Hutchins, 1995). It is found from montane to alpine grassland in the North and South Island (Poole & Adams, 1994). Shoots here tested were acquired from a plant growing outdoors at Hörsholm Arboretum in Denmark, November 2006. It was originally collected as seeds by Poul Söndergaard in New Zealand, 1975. Parent grew in Canterbury, westslope of Mount Sugarloaf, Cass, at 650 m altitude (Jerry Leverenz, pers. comm.).

Coprosma virescens

Shrub up to 3 m tall with 5-8 mm long, spathulate-oblong thin leaves. (According to Wilson & Galloway (1993) it may form a small tree up to 6 m tall with slender branchlets). Partly deciduous. Yellowish white translucent drupe, 6 mm long. Grows in lowland scrub of southeastern North Island and eastern South Island (Poole & Adams, 1994).

Olearia

Olearia clearly belongs to Asteraceae as seen from its daisy flowers. Being shrubs and small trees they are deservedly known as tree daisies. Most species have white ray florets, although shades of purple occur. There are about 30 species in New Zealand, and the rest of the totally 130 species mainly grow in Australia. In New Zealand they grow from seashore through forests and up in subalpine regions. Leaf shape varies widely between species. Hybrids with intermediate leaf forms are found in the wild (Poole & Adams, 1994). Most are easily grown

and propagated from cuttings, although they can be prone to sudden collapse during prolonged drought in the summer. Heads (1998) recognised a section (*Olearia* sect. *Divaricaster*) within New Zealand *Olearia*. They are distinguished by features like having small opposite leaves on short shoots, long shoots which abort apically, flowers with purple style arms and an insect fauna of host-specific Lepidoptera. Two of the species tested here, *O. odorata* and *O. solandri*, belong in that section. In total nine species were freeze tested and all except *Olearia odorata* were bought as large rooted cuttings from Ben Rushbrooke of Garden Cottage Nursery in Scotland, June 2006. All except *O. odorata* are evergreen. Most of them want full sun and moist well-drained soil, although some will tolerate shade and some will prefer dryer soil (Ben Rushbrooke, pers. comm.). A mainly coastal species growing in forests and scrub and not tested here, *Olearia paniculata* had leaves resistant to –7°C according to Bannister (2003).

Olearia capillaris

Shrub reaching 1 m. Divaricating. Leaves 0.5-1.5 cm long, about orbicular. Distributed in the southern North Island to central South Island: montane to subalpine in forest margins and by stream sides (Poole & Adams, 1994). Ben Rushbrooke (pers. comm.) says it can become 2 m tall and is tight divaricating.

Olearia x haastii

Probably a hybrid between *O. avicenniifolia* and *O. moschata*. It can reach 3 m and has leaves 1.5-2.5 cm long, oblong-ovate. Can be found from Arthur's pass to central Otago in montane to subalpine scrub (Poole & Adams, 1994). It is probably the most commonly planted *Olearia* in the UK, maybe as it is very frost hardy and pollution tolerant (Ben Rushbrooke, pers. comm.). Sakai & Wardle (1978) found frost resistance in the *O. avicenniifolia* to be –10°C for leaf and bud, and –13°C for cortex.

Olearia x macrodonta 'Major'

A hybrid between *O. arborescens* and *O. ilicifolia*. The hybrid can reach 7 m in New Zealand. Leaves 5-10 cm long, broad ovate, sharply and coarsely toothed, bearing resemblance to those of *Ilex aquifolium*. Montane to subalpine forest of North and South Island (Poole & Adams, 1994). This cultivar is strong growing and tolerates sea wind and shade (Ben Rushbrooke,

pers. comm.). Leaves of *O. arborescens* and *O. ilicifolia* were found resistant to –8.4°C and –9.6°C, respectively (Bannister, 2003).

Olearia moschata

Shrub up to 4 m tall with musky fragrance and greyish green leaves, which are 1-2 cm long, obovate-oblong. Montane and subalpine scrub in Arthur's Pass to Central Otago (Poole & Adams, 1994).

Olearia nummularifolia var. *nummularifolia*

Shrub reaching 3 m (often only 1 m; Wilson & Galloway, 1993) with branchlets viscid. Leaves small, 5-12 mm long, and close set with margins recurved (Poole & Adams, 1994). Montane and subalpine scrub of the North- and South Island, and lowland in Stewart Island (Wilson & Galloway, 1993). *O. num.* var. *cymbifolia* is local in the South Island mountains (Poole & Adams, 1994). Bannister (2003) found the leaf frost resistance of *O. nummularifolia* to be –9.3°C.

Olearia odorata

The only deciduous species tested. Shrub reaching 4 m with stout branches and leaves 1-2.5 cm long, usually in opposite fascicles. Few flower heads, fragrant and with bracts viscid. Grows in montane and subalpine shrubland in Canterbury, Westland, and Otago (Poole & Adams, 1994). Branches tested were cut from a plant that has been growing in the rock garden of Gothenburg Botanic Garden for ca 30 years. It was originally collected as seeds from the Pisa Range in Central Otago, on the track to Lake McKay, at 700-1700 m altitude (Henrik Zetterlund, pers. comm.). Hugh D. Wilson (pers. comm.) confirmed this shrub to be *O. odorata*.

Olearia x oleifolia 'Oleifolia'

Maybe a hybrid between *O. avicenniifolia* and *O. odorata*. A shrub to ca 1.2 m in height with leaves ca 4-7 cm long and 0.7-2 cm wide, greyish green above and white beneath. Collected in the upper Rangitata River, Canterbury, in 1869 (Metcalf, 2000).

Olearia solandri

A shrub reaching 5 m with branchlets and underside of leaves having yellowish pubescence. Leaves 5-8 mm long, linear-oblong. It grows in shrubland of lowland and montane districts mainly near the coast in North Island and northern South Island (Poole & Adams, 1994). It has a marzipan fragrance when in flower and on cold winter days (Ben Rushbrooke, pers. comm.).

Olearia traversii

This shrub from Chatham Islands can get 10 m tall and is widely used as a hedge plant. The glossy green leaves are 4-6.5 cm long, oblong to ovate-oblong, opposite on square branchlets (Poole & Adams, 1994). It is fast growing, tolerates pure sand and is very tolerant to sea wind (Ben Rushbrooke, pers. comm.).

Podocarpus

Podocarpus is a large genus (ca 100 species; Poole & Adams, 1994) of succulent fruited evergreen conifers within Podocarpaceae. The family is mainly distributed in the Southern Hemisphere but has representatives in Japan and the Himalayas (Hutchins, 1996). There are four species of *Podocarpus* in New Zealand; but the family Podocarpaceae is well represented by more genera in the country: *Phyllocladus*, *Dacrydium*, *Dacrycarpus*, *Prumnopitys*, *Halocarpus*, *Lagarostrobus* and *Lepidothamnus*. Some are small shrubs and others are tall timber trees (Poole & Adams, 1994). In *Podocarpus* the seeds are situated on swollen foot stalks, red berry like receptacles. Flowers are separated onto male and female plants, and for female plants to develop fruit male plants are needed. They are wind pollinated. *Podocarpus* have root nodules with nitrogen fixing bacteria (Hutchins, 1996). Some of the New Zealand species are known to hybridise with each other, exemplified by the tree *P. hallii* hybridising with the shrub *P. nivalis* (Poole & Adams, 1994).

Podocarpus nivalis

A low growing shrub in the New Zealand mountains. It mainly gets 30-60 cm tall and several meters wide. One of the main differences to the Australian counterpart is the leaf tips which are usually abruptly narrowed to a sharp point. This and the next species are best grown in sunny well-drained situations, and are also suitable for containers (Hutchins, 1996). Poole & Adams (1994) describe leaves as 0.5-1.5 cm long. The plants named ‘A’ and ‘B’ in this report

are ten-year-old seedlings from mother plants growing at Hörsholm arboretum in Denmark. The mother plants were propagated from cuttings collected in 1975 from Craigieburn mountains, Broken Hill Ski Area, Canterbury, at an altitude of 1300 m. Frost resistance in this species has formerly been measured to –22°C for leaf and twig, and –20°C for bud (Sakai & Wardle, 1978). It has been considered hardy to Swedish zone 2 (Lorentzon, 1996).

Podocarpus lawrencei 'Blue Gem'
This species is an exception to the limitation to New Zealand flora since it comes from Tasmania and southeastern Australia, where it is usually found among rocks in the mountains. It closely resembles *P. nivalis* though. The cultivar 'Blue Gem' is one of the two female forms of this species which have been grown in Britain for many years. This cultivar has blue-green leaves (Hutchins, 1996). The species is supposed to be hardy to Swedish zone 2 (Lorentzon, 1996). The material tested was bought from a garden centre, Åkarps Allväxtcenter, in southern Sweden. They had bought plants from the Netherlands (Eva Karlsson, pers. comm.).

Podocarpus 'County Park Fire'
This is a PBR (Plant Breeder's Rights) -protected hybrid between *P. lawrencei* and *P. nivalis* developed by Graham Hutchins in England. New shoots and needles are colourful, changing with the light, temperature and fertilisers. The material tested was bought from a garden centre, Åkarps Allväxtcenter, in southern Sweden. They had bought plants from the Netherlands (Eva Karlsson, pers. comm.).

Other plants tested

Reference plants were partly randomly chosen, but were often included because of good availability of shoots. All of them were included because of curiosity of how much frost they could tolerate under circumstances given. Their main value is for putting the frost resistance measured in New Zealand species into perspective. All except *Hebe salicifolia* are known to survive winters in the mildest parts of Sweden.

Buxus sempervirens 'Rotundifolia'
A large evergreen shrub, 3-5 m tall. Hardy in Swedish zone 3 (Lorentzon, 1996). Bärtels & Roloff (2006) list the species to USDA zone 6.

Calluna vulgaris ‘Darkness’

A small evergreen shrub 0.2-0.35 m tall. A cultivar indicated as hardy to Swedish zone 3, while the species is hardy throughout Sweden to zone 8 (Lorentzon, 1996). Bannister & Polwart (2001) measured a maximum frost resistance of –22°C in the species in Britain.

Hebe salicifolia

A representative of the largest genus of flowering plants in New Zealand. Material used has come from several large potted 1-year old seedlings of the species. The provenance of material tested is Southland. It is a large leaved (willow like thin leaves) evergreen species and has flowers in inflorescences longer than leaves, indicated as hardy in USDA zone 7 by Chalk (1988), although not grown in Sweden to my knowledge. Grows wild up to 1000 m in New Zealand. The frost resistance of leaves in July (Dunedin, NZ) has earlier been determined to –6°C (Bannister, 1990).

Lonicera nitida ‘Elegant’

An evergreen shrub up to ca 1 m tall. The species is a native of Yunnan and West Sichuan and tolerates about –15°C (Phillips and Rix, 1994), but hardy in Swedish zone 2 according to Lorentzon (1996) which would be indicative of a slightly larger frost resistance.

Phyllostachys aurea

This species belongs to a genus of bamboos from lowland China with a continental climate making them withstand hot summers and cold winters. It is supposed to get 8 m tall in a good climate with a culm thickness of 4 cm. Cold hardiness is –20°C (Bell, 2000). Top part of shoots used for freeze testing were cut from a plant which has been growing ca 15 years at Vemmenhögsgården in southernmost Sweden. Leaves are often damaged in the late winter, probably due to frost desiccation in the strong sun.

Taxus baccata

This genus somewhat resembles *Podocarpus* but is differing in a number of characteristics. They are placed in separate families (Taxaceae and Podocarpaceae). *Taxus* is very poisonous. This species may become a 10-12 m high tree and is naturally distributed in Europe, Caucasus and northern Africa. It is listed as USDA zone 6 (Bärtels & Roloff, 2006) and hardy in

Swedish zone 4, while several cultivars are less winter hardy (Lorentzon, 1996). Frost resistance measured in winter buds of *Taxus* spp. ranged from –15 to –30°C. This may be compared to winter buds of *Podocarpus* spp. which range from –4 to –22°C and *Pinus* spp. which range from –5 to –70°C (Sakai, 1983).

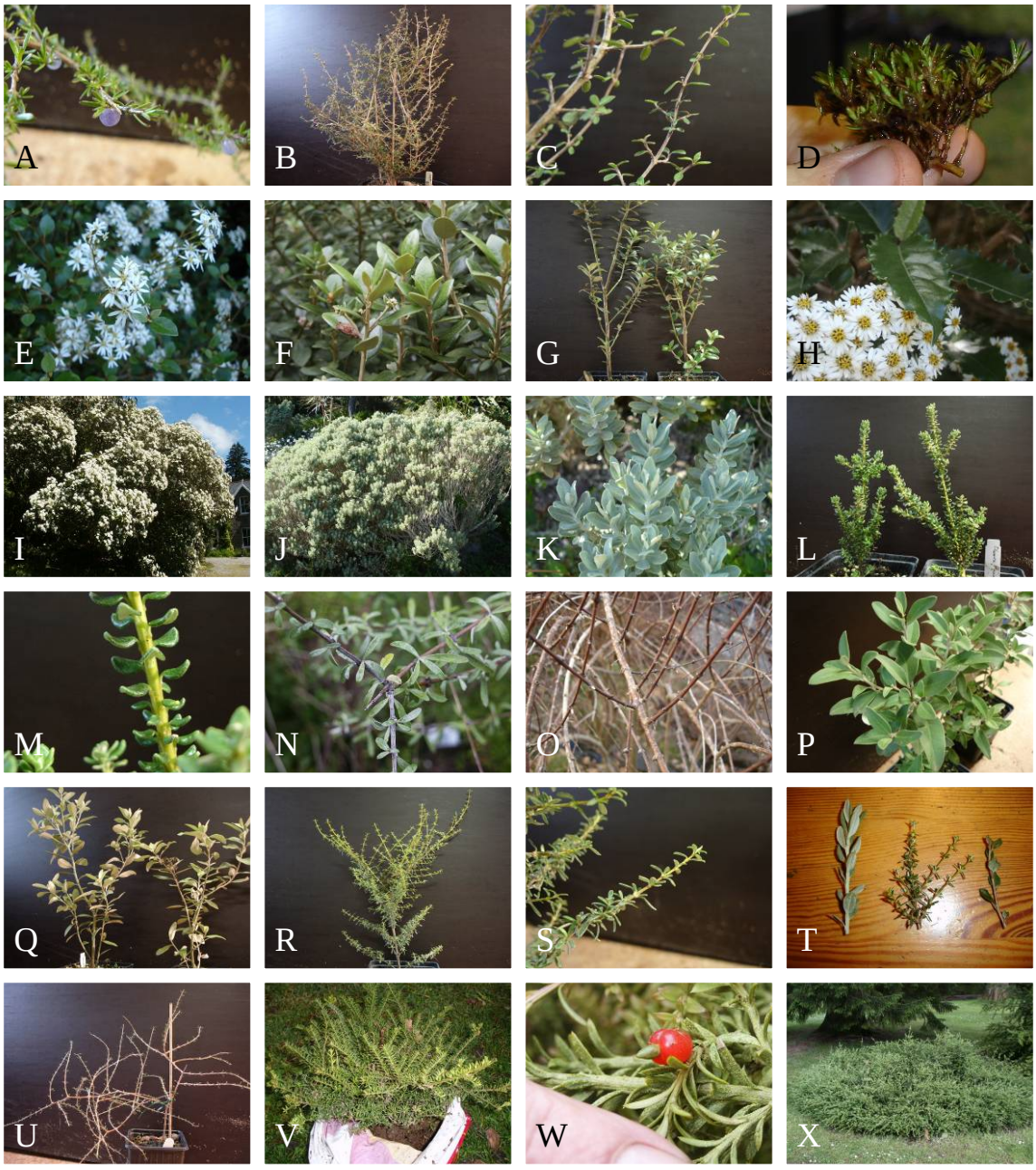

Figure 2. Plant material. A. *Coprosma acerosa v. brunnea* 'Blue Beauty'. B+C. *Coprosma dumosa*. D. *Coprosma petriei*. E. *Olearia capillaris*. F+G. *Olearia x haastii*. H+I. *Olearia x macrodonta* 'Major'. J+K. *Olearia moschata*. L+M. *Olearia nummularifolia v. num*. N+O. *Olearia odorata*. P+Q. *Olearia x oleifolia* 'Oleifolia'. R+S. *Olearia solandri*. T. Olearias from left: *O. moschata, O. solandri, O. capillaris*. U. *Coprosma virescens*. V+W+X. *Podocarpus nivalis*. Photos by author.

Plant material treatments

Most of the plant material was potted plants held outdoors in southern Scania (55°30'N) in the autumn and winter 2006/07. They were grown in peat- and perlite mixtures with some sand and were moderately fertilised. The plants were allowed to cold acclimate with the natural shortening day lengths and decreasing temperatures. They were exposed to the first frost on November 1-2 2006. It was rather severe for being the first frost, dropping to ca –5°C. Temperatures in October had been 5-15°C and never close to frost. After the first frost potted plants were brought into a cool building for protection. Since weather became mild plants were brought outdoors again two weeks later. They were exposed to temperatures of 5-12°C in November, and by the end of the month shoots of some plants were freeze tested. Some shoots tested did however come from plants that had been growing in Hörsholm arboretum north of Copenhagen in Denmark and in Gothenburg botanical garden, acclimated to climatic circumstances there. Danish contributions were shoots from *Podocarpus nivalis* 'A', 'B' and *Coprosma petriei,* while shoots from *Olearia odorata* came from Gothenburg. Climatic differences during autumn were assumed to be small. The next freeze tests were in mid-January. Shoots of all plants except one then tested had been exposed to the same climate from the end of November to mid-January. The exception again was *Olearia odorata* growing outdoors in Gothenburg botanical garden. December was generally very mild in southern Scania with temperatures above zero, except some light frosts by Christmas, but below 10°C. Plants were brought indoors for some days close to Christmas but soon brought out again. They were only exposed to one light frost by Christmas. Plants were kept outdoor until mid-January when the tests were run again. No frosts were interrupting and temperatures stayed above zero and some days went up to 10°C. Control plants *Buxus sempervirens* 'Rotundifolia', *Taxus baccata*, *Lonicera nitida* 'Elegant' and *Phyllostachys aurea* were growing outdoors in the ground in southern Scania all the time.

Freezing

Top shoots ca 4-20 cm long were cut from the plants to be tested and put in polythene bags which were closed after the contents had been given a spray of distilled water (see figure 3). Single shoots from one to five taxa was included in each bag (meaning there were 1-5 shoots/bag). In the case of *Olearia odorata* shoots were rather taken 20 or 40 cm from the

tips, discarding the outer part, and had a diameter of ca 2-3 mm. Either three or five shoots were cut from each taxon for each treatment, meaning a taxon was represented in three or five bags/freezer. With six treatments this meant 18 or 30 shoots per taxon and test session. See tables 3 and 4 for taxa tested, when they were tested, how many shoots were included in the treatments, and what minimum target temperatures were reached in respective treatments. Bags were held at 3-10°C in moderate to low light for one to two days before subjected to freeze treatments. At the time for freezing, control bags not to be frozen were placed in a cool and dark frost-free place. All the other bags were hanged on metal sticks in the upper part of five freezers. A temperature probe (Tinytag) was included in each freezer for monitoring actual frost temperatures at the shoots (figure 3D). Table 4 shows that minimum target temperatures reached varied between different sessions. Large differences between sessions were intentional, like between sessions 1 and 2 where the supposedly less cold resistant taxa were only included in session 1 and *vice versa*. This was in order to try to expose shoots to non-damaging as well as largely damaging temperatures. Smaller differences, like between sessions 1 and 3 where due to inaccuracies of the freezing equipment. Freezers belonged to the Swedish forestry institute SkogForsk in Ekebo. They had fans in the bottom to distribute the air and provide an even temperature. Freezers were connected to a computer programmable for deciding freezing rates and duration. Shoots were first cooled from room temperature to 2°C at a rate of 10°C/h, and then to respective target freezing temperature at a rate of 5°C/h. Target temperatures were held for 3 hours and then temperature increased by 10°C/h until 2°C was reached again. It was held until all freezers had reached this level, and 2 h more. Temperature rates and duration of target temperature were according to Stener *et al*. (2002). The last step was for all freezers to increase temperatures at a rate of ca 10°C/h. In practice temperatures increased at this rate up to ca 10°C, while the last warming to room temperature went faster because the freezer lid was opened. Target temperatures in different freeze sessions were chosen to inflict no damage at highest temperature and large damage at lowest temperature.

Table 3. Plants freeze tested in November and/or January. (n)= number of shoots of one taxon tested in parallel in each freeze-treatment. Freeze sessions are given names of 1-5. See table x for minimum temperatures reached in each session plus session dates.

Taxon	n	Month(s) tested	Freeze session(s)
Coprosma brunnea 'Blue Beauty'	3	Nov + Jan	2+3
Coprosma dumosa	3	January	3
Coprosma petriei	3	November	2
Coprosma virescens	3	January	3
Olearia capillaris	5	November	1
Olearia x haastii	5	Nov + Jan	1+3
Olearia x macrodonta 'Major'	5	Nov + Jan	1+3
Olearia moschata	3	Nov + Jan	1+3
Olearia nummularifolia var. *nummularifolia*	3	January	3
Olearia odorata	5	Nov + Jan	1+4
Olearia x oleifolia 'Oleifolia'	3	Nov + Jan	1+3
Olearia solandri	5	November	1
Olearia traversii	3	January	3
Podocarpus 'County Park Fire'	5	January	5
Podocarpus lawrencei 'Blue Gem'	5	January	5
Podocarpus nivalis 'A' ex. Hörsholm	5	Nov + Jan	2+4
Podocarpus nivalis 'B' ex. Hörsholm	5	Nov + Jan	2+4
Reference species and other:			
Buxus sempervirens 'Rotundifolia'	5	Nov + Jan	2+4
Calluna vulgaris 'Darkness'	5	January	5
Hebe salicifolia	3	January	4
Lonicera nitida 'Elegant'	5	January	5
Phyllostachys aurea	3	January	5
Taxus baccata	5	Nov + Jan	2+4

Table 4. Freeze sessions with actual minimum temperatures reached (°C).

Session no.:	1 (November)	2 (November)	3 (January)	4 (January)	5 (January)
Dates:	27-28/11 2006	28-29/11 2006	15-16/1 2007	16-17/1 2007	22-23/1 2007
Control	>0	>0	>0	>0	>0
Freezer 1	-3.1	-6.7	-3.6	-6.7	-7.2
Freezer 2	-8.2	-11.8	-8.2	-11.8	-12.3
Freezer 3	-12.9	-16.4	-12.9	-17.0	-17.6
Freezer 4	-18.3	-21.8	-18.3	-25.7	-25.7
Freezer 5	-22.7	-29.6	-23.2	-36.2	-35.7

Electrolyte leakage assessment

Once the freeze sessions were finished bags were brought to the Swedish University of Agricultural Sciences in Alnarp. Stem segments, one cm long, were cut out from all shoots and placed in individual test tubes (polypropylene vials) containing 10 ml ultra pure water (millipor). See figure 3E. The procedure was to take away any leaves and side shoots from the lower part of the shoot, rinse it briefly with ultra pure water, and cut off the lower 1-5 cm (depending on shoot size). This part was discarded, while 1 cm of the new base was measured, cut and placed in a test tube. This piece was generally either last year or second year wood. The remaining top part of the shoot was placed back into the plastic bag, which was closed and stored in a cool place (5-10ºC) for later visual inspection. Most of this procedure was according to Stener *et al*., 2002. Five test tubes containing only ultra pure water were included for control. Test tubes were enclosed with polythene film (to prevent evaporation and contamination) and aluminium foil and placed on a shaker in room temperature (according to Stattin, pers. comm.) until the next day.

On the next day the conductivity of water with stem segments was measured with a conductivity meter having a temperature-compensating probe (EcoScan CON5, Eutech instruments, see figure 3F). Time periods for leakage are according to Colombo *et al*. (1995) who suggested 18-24h. 19.5-23h was used here. See more time details in table 5. A special lid, not tight, was placed on test tubes. The tubes were then autoclaved at ca 1.2 bar and 120ºC for 2h (according to Stener *et al*., 2002), although this time was reduced to 20 minutes for tests made in January. An experiment had been set up which confirmed stem segments did not leak more after 2h autoclaving compared to 20 minutes. When the main autoclave program was finished tubes were allowed to cool. Cooled tubes were covered with polythene film and aluminium foil and placed on the shaker again. Second conductivity measurements were made the next day. Samples were then discarded. Water volume in the water control test tubes was also measured.

Table 5. Time details for injury assessments.

Freezing session finished – stem segment in water	2-6.5 h
Time on shaker before EC measurement 1	17-18.2 h
Time required for EC measurement 1	1.5-2.5 h
Autoclaving, main program	2 h or 20min
Cooling before put on shaker (inside and outside of autocl.)	1.2-2.17 h
Time on shaker before EC measurement 2	18.25-20 h
Time required for EC measurement 2	1.5-2.5 h
Stems in water until EC measurement 1	19.5-22 h
Stems in water from autoclaving to EC measurement 2	20.5-23 h
Freezing session finished – visual inspection 1	3.5 days
Freezing session finished – visual inspection 2	7.5 days

Figure 3. Moments of method. A. Shoots were cut. B. Shoots were enclosed in plastic bags and (C) placed in computerised freezers having (D) fans and thermometers. E. After freezing procedure 1-cm stem pieces of shoots were cut and placed in 10 ml of water and (F) the electric conductivity was measured before and after autoclaving. Photos by author.

Index of Injury and LT_{50} from conductivity (EC) data

Conductivity raw data were treated in Excel. Electrolyte impurities from water or tubes were subtracted, and a small volume loss at autoclaving compensated for. Index of Injury (I_t) was calculated according to Flint *et al.* (1967) for every stem segment:

$$I_t = \frac{100(RC_{frozen} - RC_{control})}{1 - RC_{control}}$$, where

$RC_{frozen} = EC_{frozen} / EC_{frozenkilled}$
$RC_{control} = EC_{unfrozen} / EC_{unfrozenkilled}$
EC = electric conductivity of elute

$RC_{control}$ used in all calculations was an average of generally three or five $RC_{control}$ values for respective taxon. $RC_{control}$ average is used to give the electrolyte leakage of undamaged tissues an Index of Injury of ca 0%. One does however have to watch out with the control shoots, because if they do have any damage it will lead to an overestimation of frost resistance via Index of Injury (Eva Stattin, pers. comm.).

Index of Injury was plotted against actual minimum temperatures measured in freezers. In theory an Index of Injury of 50% would equal LT_{50}, but since electrolyte leakage was always greater from autoclaving than 100% frost injury and the maximum Index of Injury varied with species, another system resembling that of Sutinen *et al*. (1992) was used. Mean I_t was plotted against minimum temperatures and LT_{50} interpolated from halfway between estimated maximum frost injury and no frost injury. This LT_{50} was assumed to be the frost resistance of the stem. Additionally, I_t data from some of the species was fitted to a sigmoid curve, using a regression with the logistic function. It was used despite Verwijst & von Fircks (1994) concluded the more flexible Richards function was to be preferred. The model used here was:

$$Y = \frac{\max injury}{1 + \left(\frac{x}{LT_{50}}\right)^{-slope}}$$, where

Y = Index of Injury

Max injury = maximum frost injury
x = freezing temperature
LT_{50} = Frost resistance temperature

Autoclave time trial

An experiment was designed to determine whether the 2-hour autoclave time for stem segments could be lowered. In December, 42 about 20 cm long top shoots each of *Taxus baccata* and *Buxus sempervirens* 'Rotundifolia' were cut in southern Scania. They were distributed into two large plastic bags, half of the shoots of each species in each bag. Shoots were sprayed with distilled water. One bag was kept in 5-10ºC overnight, while the other was placed into a regular freezer at –18ºC. The bag was removed from the freezer after 11h and thawed to room temperature within 30 minutes. The plan was to make procedures according to the electrolyte leakage method with frozen and unfrozen stem segments from both species. Only the autoclave time for killing stem tissues was either 20, 40 or 120 minutes. Seven stem segments (n=7) of each species and freeze-treatment group were tested at each autoclave time period. One-cm stem segments had been cut and placed in 10 ml water and placed on shaker before. Conductivity was measured 22h after they were placed in water. Tubes were replaced on the shaker after respective autoclave treatment, and conductivity was measured 22h after autoclave main program had stopped. Relative conductivity was calculated as conductivity before autoclaving divided by conductivity after autoclaving for each stem segment. Results were compared within species and freeze-treatment groups between the different autoclave treatments using ANOVA unstacked.

Visual injury assessment

After stem segments had been cut out the remaining top part of shoots were put back in the closed plastic bags. Shoots were sprayed with distilled water to prevent them from desiccating before visual assessments. Storage conditions were in moderate to low light. Those assessed in November were first stored in 5-10ºC for 3.5 days and then in room temperature the last 4 days before final visual assessment. In January shoots were stored in room temperature all the time, but final visual assessment was 7.5 days after freezing at both occasions. A first preliminary assessment was always done 3.5 days after freezing. All shoots including unfrozen controls were inspected and scored 0-100 % for leaf damage and 0-100% for stem

damage. Scores were given subjectively, mainly according to tissue blackening or browning compared to unfrozen controls. At the second time of scoring, shoots from unfrozen control and the most deeply frozen shoots were scored first to give an idea of what no damage and severe damage looked like. See figure 4 for examples of frost injured shoots.

If 50% of leaf areas looked damaged, this was a 50% score. If 50% of leaves looked completely damaged, while the rest looked rather unaffected, this was a 50% score. This method of scoring is close to that used by Bannister & Lee (1989) and Bannister & Polwart (2001). Stem tissues were more difficult to score but dissecting the stem on a few places generally gave a rather good idea. Apart from discoloration of especially phloem and cambium but also xylem, a species specific smell could sometimes be noticed from damaged stem tissues and leaves. Most dicotyledonous species showed some leaf fall when damaged. A good indicator of damage is the growth of grey mold on leaves or stems at inspection two. Grey mold (*Botrytis cinerea*) never grew on undamaged tissues at this time. It was especially helpful with some species, like *Buxus*, which sometimes had almost no discoloration at all, but still was damaged. Most scores ended up at 0 or 100% damage, which are generally rather certain figures for telling the chances of these tissues survival. Intermediate scores of e.g. 10-20% tell of damage but not lethal, while 70-90% tells of no complete destruction, but still probably lethal. Scores are left blank in case of large uncertainty. Otherwise leaf and stem scores from inspection two were plotted against actual minimum temperatures and interpolated at 50% damage to give approximate LT_{50}-temperatures for leaves and stems.

Figure 4. Severely frost damaged plant tissues to the right in each picture, with healthy controls to the left. These visual assessments were made 3.5 or 7.5 days after freeze treatments. A. *Podocarpus nivalis*. B. *Olearia x haastii*. C. *Olearia moschata*. D. *Olearia odorata*. Photos by author.

Results

Approximate frost resistances, LT_{50}, in shoots and leaves of all species tested are presented in table 6. A low temperature, like ca –20.1°C for the stem of *Olearia odorata* in November, is indicating a comparatively high (= good) frost resistance. So a resistance to a lower temperature indicates a greater frost resistance. These figures can be compared in several ways. But first of all it shall be stated that dose response curves for frost injury, from which LT_{50} is derived, were found to be of sigmoid shape (see figures 5 & 6). When using the electrolyte leakage method (EC) and Index of Injury the relative electrolyte leakage at maximum frost injury was found to differ between taxa. It was often around Index of Injury 70-80, like in the example of *Olearia moschata* in figure 5, but sometimes much lower like I_t = 50 for young stems of *Olearia solandri* in November or I_t = 56 for stems of *Olearia odorata* in January. That reflects a higher leakage of electrolytes after tissues have been autoclaved compared to after maximum frost injury.

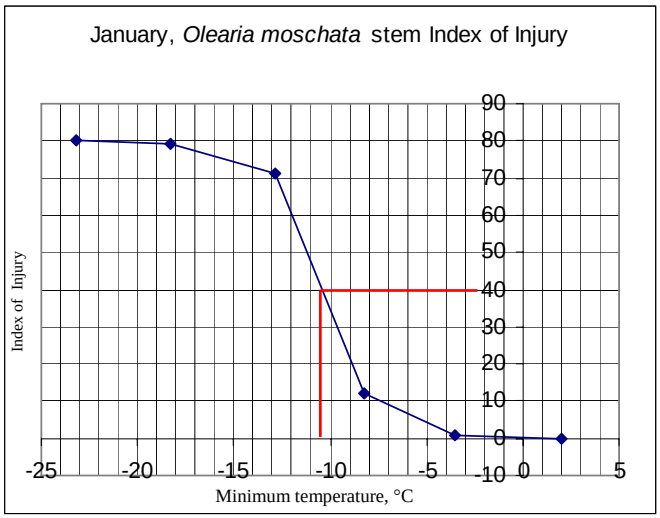

Figure 5. *Olearia moschata* stem Index of Injury in January 2007. Mean values (n=3) of Index of Injury plotted against minimum temperature (°C) shoots have been exposed to. The maximum level of frost damage ended up at about Index of Injury = 80. LT_{50} was interpolated to –10.4°C. When fitted into the logistic function the LT_{50} was calculated to –10.1°C. Approximate 95% confidence intervals for the logistic LT_{50} were ± 0.6°C.

A spectrum of frost resistances is found in the genera tested. If including both stem and leaf resistances, the former decided with two methods, this is the result from the study: *Coprosma* –5.9 to –12.7°C, *Olearia* –5.5 to –21.3°C, and *Podocarpus* –11.5 to –19.8°C. Both November and January resistances are included. For detailed comparisons between genera and taxa tested see stem frost resistance ranks in table 7, and comments on them ahead.

Table 6. Frost resistance as °C in shoots and leaves from New Zealand shrubs and reference species. The shoot frost resistance was determined with two methods in November and January.
Stem EC = LT_{50} interpolated from injury data obtained from stem pieces with the electrolyte leakage method. Stem visual and Leaf visual are LT_{50} values interpolated from injury data based on visual assessment of shoots 7.5 days after freezing.

	November 2006			January 2007		
	Stem EC	Stem visual	Leaf visual	Stem EC	Stem visual	Leaf visual
Coprosma brunnea 'Blue Beauty'	-12.7	-9.5	-9.6	-12.3	-11.2	-10.5
Coprosma dumosa	-	-	-	-11.4	-10.6	-10.5
Coprosma petriei	-12.3	-**	-10.3	-	-	-
Coprosma virescens	-	-	-	-10.1	-5.9	-5.9
Olearia capillaris	-6.0	-5.7	-5.7	-	-	-
Olearia x *haastii*	-12.0	-11.1	-9.7	-15.5	-15.4	-10.5
Olearia x *macrodonta* 'Major'	-9.9	-9.2	-7.8	-11.1	-10.7	-10.3
Olearia moschata	-9.3	-6.2	-5.7	-10.4	-10.3	-9.0
Olearia nummularifolia var. *nummularifolia*	-	-	-	-9.7	-10.2	-9.2
Olearia odorata	-20.1	-20.3	(dec.)	-20.8	-21.3	(dec.)
Olearia x *oleifolia* 'Oleifolia'	-9.8	-10.4	-6.2	-14.6	-12.3	-10.1
Olearia solandri	-9.9	-**	-9.9	-	-	-
Olearia traversii	-	-	-	-8.0	-5.5	-5.8
Podocarpus 'County Park Fire'	-	-	-	-19.8	-16.6	-14.9
Podocarpus lawrencei 'Blue Gem'	-	-	-	-17.0	-17.2	-11.5
Podocarpus nivalis 'A' ex. Hörsholm	-16.1	-14.2	-14.1	-19.4	-16.6	-16.3
Podocarpus nivalis 'B' ex. Hörsholm	-17.4	-14.7	-14.8	-17.6	-16.1	-15.7
Reference species and other:						
Buxus sempervirens 'Rotundifolia'	-21.5	-**	-28.0	-18.8	-**	-21.0
Calluna vulgaris 'Darkness'	-	-	-	-16.4	-15.8	-16.9
Hebe salicifolia	-	-	-	-9.2	-9.3	-8.8
Lonicera nitida 'Elegant'	-	-	-	-14.3	-14.0	-10.7
Phyllostachys aurea	-	-	-	-28.6	-28.6	-21.0
Taxus baccata	-23.0*	-27.9	-28.3	-25.5*	-30.9	-30.1

* There is doubt whether this species was 100% frost injured by the lowest temperature, which can lead to an underestimation of frost resistance with the electrolyte leakage method.
** This tissue was very difficult to grade for damage visually.
(dec.) = deciduous species; thus no leaves to test during winter.

When comparing species tested in late November and mid-January it is best to look at resistances found by the same method to be able to say anything about a difference between the months. There is only one *Coprosma* but five *Olearia* and two *Podocarpus* to be compared between the months. Comparing both leaves and stems, the difference between the months is obvious with all taxa increasing their frost resistance marginally to several degrees. *Coprosma brunnea* 'Blue Beauty' is the only exception with a slight decrease of stem frost resistance decided by the electrolyte leakage (EC) method. The rest of the 24 comparisons to

be made are showing increased frost resistance with time. It is often only by 1-2°C, but *Olearia* x *haastii* increased stem frost resistance by ca 3.5-4.3°C (the former decided by EC and the latter visually). *Olearia* x *oleifolia* 'Oleifolia' similarly increased stem frost resistance by ca 1.9-4.8°C (visually-EC). *Podocarpus nivalis* 'A' and 'B', which are siblings, differed quite markedly with 'A' being the less resistant in November to becoming the more resistant of them in January, meaning it increased more in resistance compared to 'B'.

Leaf frost resistance was generally following the same pattern as stem frost resistance, although leaf frost resistance was often slightly poorer (see table 6). *Olearia* x *haastii* and *Olearia* x *oleifolia* 'Oleifolia' did however show at least 4°C poorer frost resistance in leaves compared to stems one of the months. A great difference was found in *Podocarpus lawrencei* 'Blue Gem' for which leaves were close to 6°C less resistant compared to stem. Such differences were also found in reference plants, with *Lonicera nitida* 'Elegant' and the bamboo *Phyllostachys aurea* having leaves 3°C and close to 8°C less resistant than stems, respectively.

Stem LT_{50} derived from the two injury assessment methods often differed. Small differences like 1°C were common and hardly a problem, but differences of over 2°C and even up over 4°C were found. This yielded a question of what to trust, further developed in the discussion. Where differences are large the frost resistance derived visually is generally poorer (closer to 0°C) compared to that from electrolyte leakage. Such large differences were observed in stems of e.g. *Coprosma virescens*, *Olearia moschata* and *Podocarpus*.

Plants have been ranked on merit of their stem frost resistances in table 7. The lists are used to see how species and genera relate to each other. Among the New Zealand species tested, *Olearia odorata* is clearly in the top with a resistance better than –20°C, while the rest of that genus is to be found further down the list at resistances of ca –6 to –12°C. In January *Olearia* x *haastii* extended this range to better than –15°C and is the second most resistant *Olearia* here tested. All the *Podocarpus* tested were more resistant than *Olearia* x *haastii* but never quite reached up to *Olearia odorata*. Frost resistance in stems of *Coprosma* was never better than –13°C.

Reference species are included in the table 7 lists. *Taxus baccata* is in the top, together with *Phyllostachys aurea* tested in January. *Buxus sempervirens* 'Rotundifolia' was up there in November but went down simultaneously with *Podocarpus* going up, and ranked among the *Podocarpus* in January. *Lonicera nitida* 'Elegant' ranked low, even with *Olearia* x *haastii* beating it in January. The soft stems of *Hebe salicifolia* were only resistant to about –9°C.

Table 7. Ranking of taxa on stem LT_{50} (°C) achieved by interpolation of data based on either electrolyte leakage assessment (EC) or visual assessment (Visual). Reference species and other (not *Coprosma*, *Olearia* or *Podocarpus*) are written in *italic* font. *Probably underestimated frost resistance, see table 6.

November stem (EC)		**LT_{50}**		**November stem (Visual)**		**LT_{50}**
1	*Taxus baccata*	-23.0*		*1*	*Taxus baccata*	-27.9
2	*Buxus sempervirens 'Rotundifolia'*	-21.5		2	Olearia odorata	-20.3
3	Olearia odorata	-20.1		3	Podocarpus nivalis 'B' ex. Hörsholm	-14.7
4	Podocarpus nivalis 'B' ex. Hörsholm	-17.4		4	Podocarpus nivalis 'A' ex. Hörsholm	-14.2
5	Podocarpus nivalis 'A' ex. Hörsholm	-16.1		5	Olearia x haastii	-11.1
6	Coprosma brunnea 'Blue Beauty'	-12.7		6	Olearia x oleifolia 'Oleifolia'	-10.4
7	Coprosma petriei	-12.3		7	Coprosma brunnea 'Blue Beauty'	-9.5
8	Olearia x haastii	-12.0		8	Olearia x macrodonta 'Major'	-9.2
9	Olearia x macrodonta 'Major'	-9.9		9	Olearia moschata	-6.2
9	Olearia solandri	-9.9		10	Olearia capillaris	-5.7
10	Olearia x oleifolia 'Oleifolia'	-9.8				
11	Olearia moschata	-9.3				
12	Olearia capillaris	-6.0				
January stem (EC)				**January stem (Visual)**		
1	*Phyllostachys aurea*	-28.6		*1*	*Taxus baccata*	-30.9
2	*Taxus baccata*	-25.5*		*2*	*Phyllostachys aurea*	-28.6
3	Olearia odorata	-20.8		3	Olearia odorata	-21.3
4	Podocarpus 'County Park Fire'	-19.8		4	Podocarpus lawrencei 'Blue Gem'	-17.2
5	Podocarpus nivalis 'A' ex. Hörsholm	-19.4		5	Podocarpus 'County Park Fire'	-16.6
6	*Buxus sempervirens 'Rotundifolia'*	-18.8		5	Podocarpus nivalis 'A' ex. Hörsholm	-16.6
7	Podocarpus nivalis 'B' ex. Hörsholm	-17.6		6	Podocarpus nivalis 'B' ex. Hörsholm	-16.1
8	Podocarpus lawrencei 'Blue Gem'	-17.0		*7*	*Calluna vulgaris 'Darkness'*	-15.8
9	*Calluna vulgaris 'Darkness'*	-16.4		8	Olearia x haastii	-15.4
10	Olearia x haastii	-15.5		*9*	*Lonicera nitida 'Elegant'*	-14.0
11	Olearia x oleifolia 'Oleifolia'	-14.6		10	Olearia x oleifolia 'Oleifolia'	-12.3
12	*Lonicera nitida 'Elegant'*	-14.3		11	Coprosma brunnea 'Blue Beauty'	-11.2
13	Coprosma brunnea 'Blue Beauty'	-12.3		12	Olearia x macrodonta 'Major'	-10.7
14	Coprosma dumosa	-11.4		13	Coprosma dumosa	-10.6
15	Olearia x macrodonta 'Major'	-11.1		14	Olearia moschata	-10.3
16	Olearia moschata	-10.4		15	Olearia nummularifolia var. num.	-10.2
17	Coprosma virescens	-10.1		*16*	*Hebe salicifolia*	-9.3
18	Olearia nummularifolia var. num.	-9.7		17	Coprosma virescens	-5.9
19	*Hebe salicifolia*	-9.2		18	Olearia traversii	-5.5
20	Olearia traversii	-8.0				

Frost resistances in table 6 and 7 have been interpolated. When using the electrolyte leakage method it can look like figure 5. It was also possible to make logistic regressions from some of these data, as seen in figure 6, from which another LT_{50} was given together with 95% confidence intervals and standard error (see table 8). Frost resistance figures from interpolation were however found to be rather close to those from logistic regression.

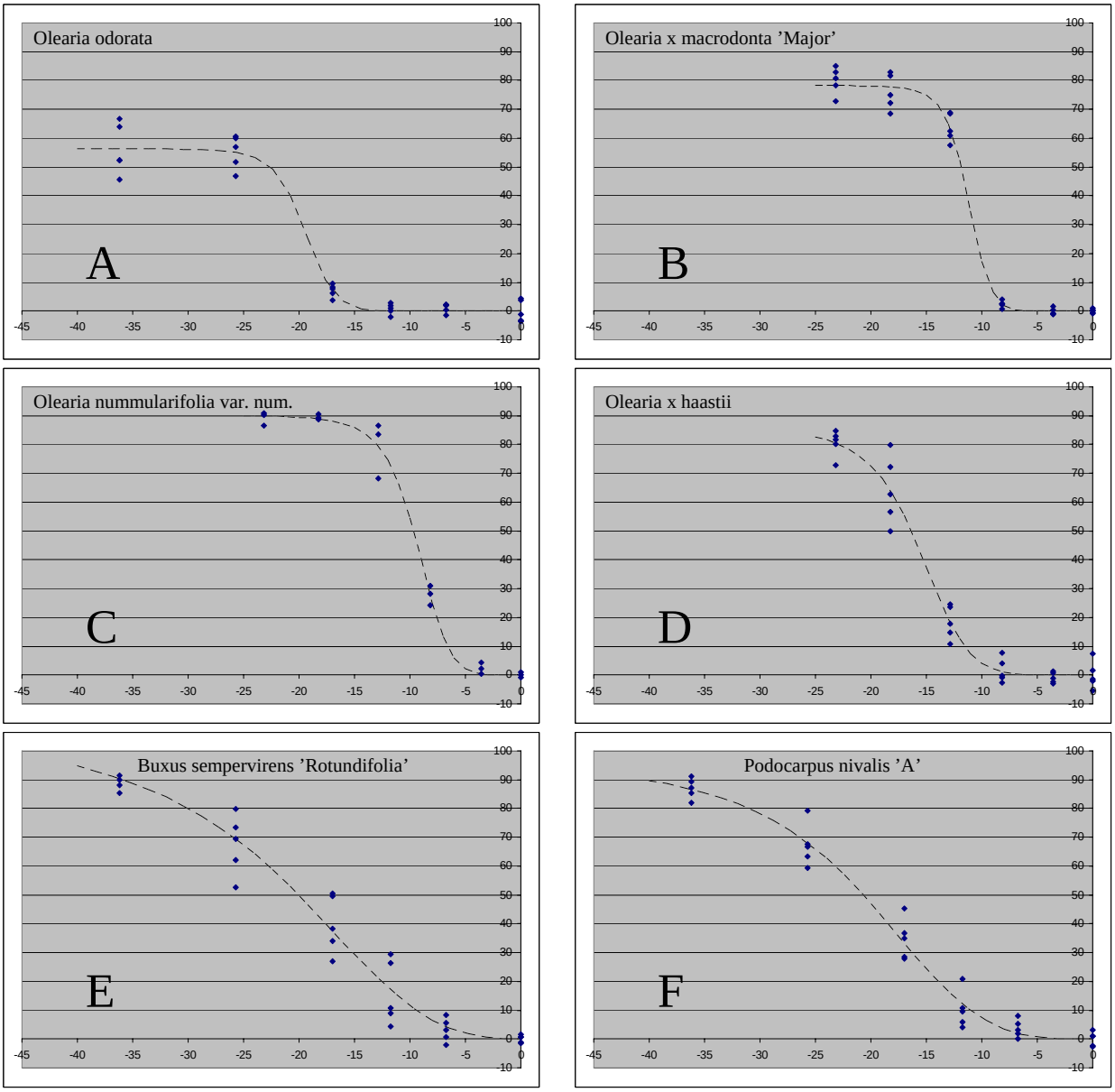

Figure 6. Stem Index of Injury (y-axis) plotted against minimum frost temperature (°C) shoots were exposed to in January. The logistic regression (S-curve) is included. A. *Olearia odorata*. B. *Olearia x macrodonta* 'Major'. C. *Olearia nummularifolia* var. *num.* D. *Olearia x haastii*. E. *Buxus sempervirens* 'Rotundifolia'. F. *Podocarpus nivalis* 'A'.

Table 8. Stem LT_{50} (°C) from logistic regression of Index of Injury data (electrolyte leakage method). Standard error and approximate 95% confidence intervals included. Stem LT_{50} via interpolation is there for comparison, otherwise seen in table 6.

November	LT_{50}	95 % conf. int.	std error	LT_{50} interpolated
Olearia x haastii	-12.3	± 0.6	0.3	-12.0
Olearia capillaris	-6.8	± 13.1	6.4	-6.0
Olearia x oleifolia 'Oleifolia'	-9.2	± 1.7	0.8	-9.8
Olearia moschata	-9.0	± 0.6	0.3	-9.3
Podocarpus nivalis 'A'	-16.7	± 0.9	0.5	-16.1
Podocarpus nivalis 'B'	-18.8	± 5.4	2.6	-17.4
January				
Coprosma brunnea 'Blue Beauty'	-12.6	± 1.0	0.5	-12.3
Coprosma dumosa	-11.0	± 2.6	1.2	-11.4
Olearia x haastii	-15.6	± 1.0	0.5	-15.5
Olearia x macrodonta 'Major'	-11.2	± 0.5	0.2	-11.1
Olearia x oleifolia 'Oleifolia'	-14.5	± 1.3	0.6	-14.6
Olearia moschata	-10.1	± 0.6	0.3	-10.4
Olearia nummularifolia var. *num.*	-9.3	± 0.5	0.2	-9.7
Olearia odorata	-19.5	± 2.7	1.3	-20.8
Podocarpus nivalis 'A'	-20.4	± 2.2	1.1	-19.4
Podocarpus nivalis 'B'	-18.3	± 2.6	1.3	-17.6
Buxus sempervirens 'Rotundifola'	-21.4	± 5.1	2.5	-18.8

Leaf and stem frost resistances were plotted against mean altitudinal ranges where the species are normally found in the wild (figure 7). The resistance seems to be rather well correlated to the altitude. The exact altitude of origin for material tested is generally not known. Using the approximate maximum altitude where species can be found would not be a good alternative since most are to be found in the subalpine belt.

It was harder to correlate frost resistance to leaf size in plants tested, as seen in figure 8. There is a tendency for small leaved plants to be more frost resistant. Many small leaved plants are however poorly frost resistant. Another way of putting it: there are no large leaved species among the most frost resistant species.

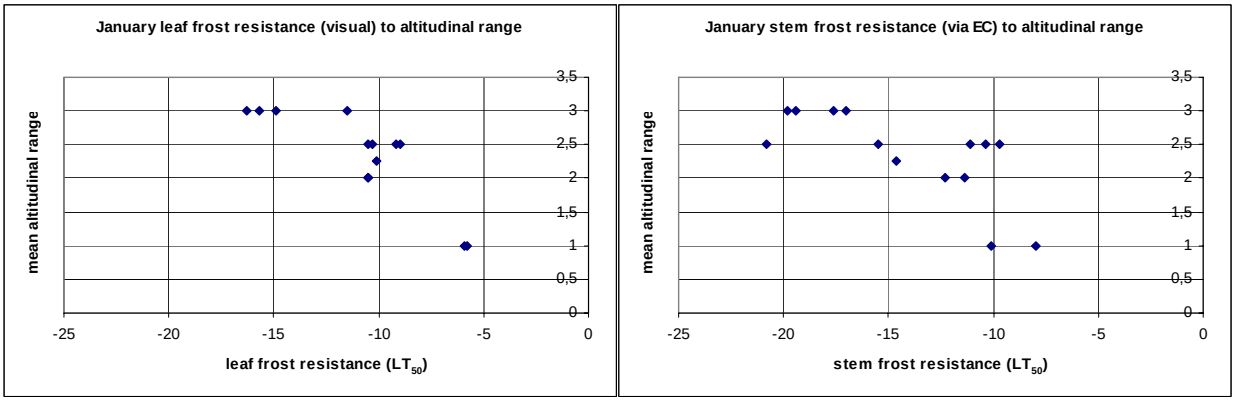

Figure 7. January frost resistances (°C) of *Coprosma*, *Olearia* and *Podocarpus* here tested plotted against mean altitudinal range. The plots are based on the same taxa except *Olearia odorata* which is deciduous and consequently not included to the left. The altitudinal range is taken according to Poole & Adams (1994), but some *Coprosma* from Wilson & Galloway (1993). Scores are Lowland=1, Montane=2, Subalpine=3, Alpine=4. Many species are present in at least two altitudinal belts and are given a mean altitudinal range score from mean of total score, according to Bannister & Lee (1989). Plotting against maximum altitude reached for species would not be that rewarding here since most species tested reach the subalpine belt.

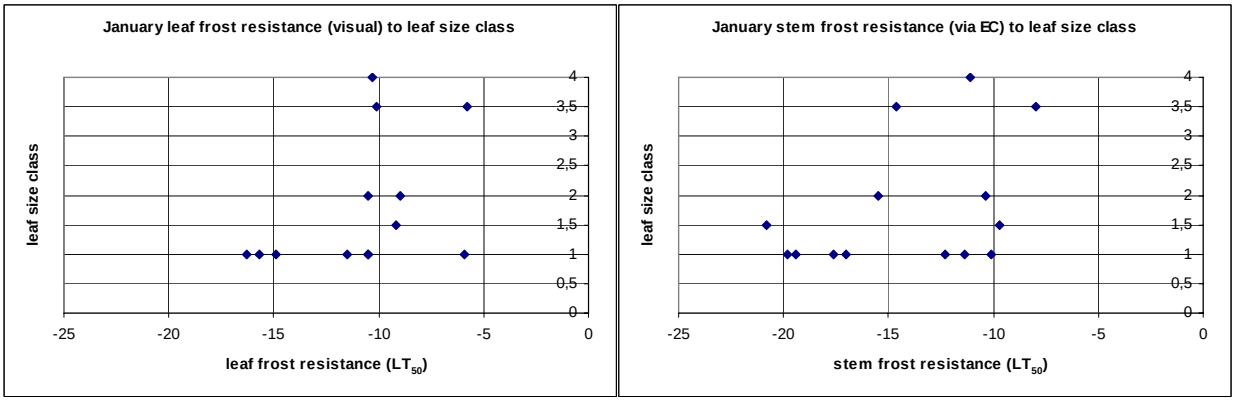

Figure 8. January frost resistances (°C) in New Zealand taxa tested as in figure 7, but plotted against leaf size class. Leaf size is here divided into four classes (1-4). 1=<0.5cm^2, 2=0.5 to 3 cm^2, 3=3 to 6 cm^2, 4=>6 cm^2. Intermediate scores were sometimes given. Leaf size was derived from same sources as in figure 7, plus Metcalf (2000).

An experiment with different periods of autoclaving for producing the total electrolytes in the electrolyte leakage method gave the following result (see figure 9). There was no significant difference of electrolyte leakage between 20, 40 and 120 minutes autoclaving in either *Buxus sempervirens* 'Rotundifolia' stems or *Taxus baccata* stems, whether frozen or not. Please notice the relative electrolyte leakage close to 10% from stems that have not been frozen (i.e. uninjured). If calculating Index of Injury according to Flint *et al*. (1967) this leakage level is denoted zero.

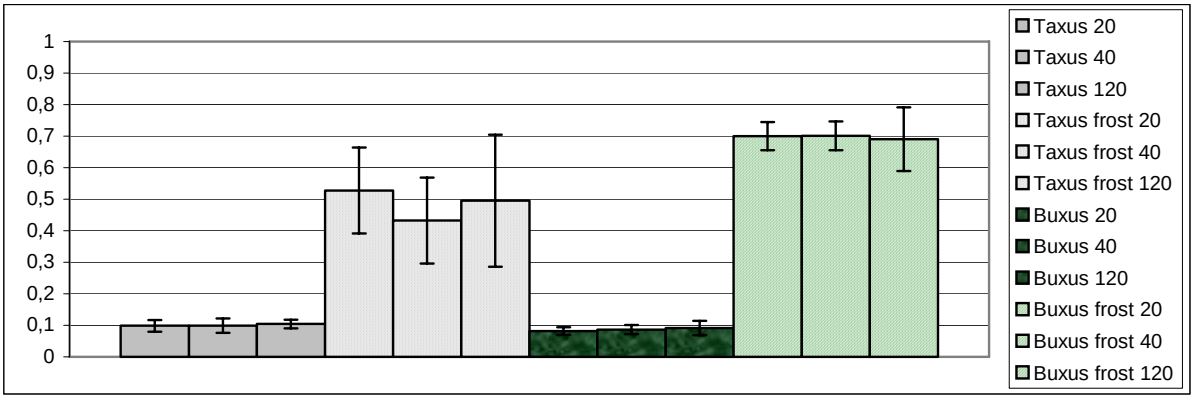

Figure 9. Relative electrolyte leakage from uninjured and frozen stems of *Taxus baccata* and *Buxus sempervirens* 'Rotundifolia' when varying the time of autoclaving between 20, 40 and 120 minutes to get maximum leakage (equalling one in this figure). N = 7. Error bars show standard deviations. Shoots were taken in mid-December and after respective treatments 1 cm stem pieces were cut out from the same season growth, ca 10-15 cm down from shoot apex with bark still green.

Discussion

Frost resistance and winter hardiness of plant material

The frost resistance recorded in shoots of most New Zealand species show that they would be intolerant to the winter temperatures of northern and central Europe. This is in accordance with experiences from other controlled tests (e.g. Sakai & Wardle, 1978; Bannister & Lee, 1989) and growing experiences with several species within the genera tested (Söndergaard, 1989; Harris *et al*., 2000). There are many factors that will make winter harder to survive, but concluded from experiences in previous studies results in this study are informative and comparable. This type of controlled freeze test study should be combined with field observations to become more valuable. Such combinations increase the understanding for mechanisms making up the total winter hardiness or lack of it. They also increase speed and accuracy in hardiness assessment.

A New Zealand shrub here tested known to have been growing and surviving in Sweden for many years was *Olearia odorata*. It was found to possess the greatest frost resistance of the New Zealand material here tested: just better than –20°C in twig tissues in both November and January (Northern Hemisphere). This was a bit of a surprise but to my knowledge no frost resistance figures have been published on this species before. This frost resistance brings it up among the absolutely hardiest woody plants of New Zealand. It places an angiosperm among the gymnosperms concluded by Sakai & Wardle (1978) to be the frost hardiest woody plants in the country, although Reitsma (1994) found leaf frost resistance in another angiosperm (*Dracophyllum filifolium*) to be greater than –20°C too. The distribution of *Olearia odorata* in the South Island in areas like Central Otago, where seed to the shrub tested was collected, is in line with a need for rather high frost resistance. I will not speculate in how it has gained this great resistance while the other *Olearia* spp. here tested have not. It seems to be hardy in southern coastal Sweden since it has been growing in the rock garden of Gothenburg Botanic Garden for three decades. Ornamental values might be considered low, but a shrub ca 2 m tall with unusually small leaves and small but nicely scented flowers could be useful at least for looking different. It could also be used in breeding work to introduce frost resistance. It should be possible to hybridise with some other species if its supposed parentage to *Olearia* x *oleifolia* is true.

All the *Podocarpus* tested, i.e. two *P. nivalis*, one *P. lawrencei* (native to Tasmania and south-eastern Australia) and one hybrid between those species, were found to have a rather high frost resistance (between –16 and –20°C for twigs in January). *P. nivalis* has earlier been found to be resistant to –22°C for leaves and twigs, and –20°C for buds (Sakai & Wardle, 1978). The material they tested was however exposed to a tougher artificial hardening regime compared to the more natural conditions here used. It would probably be enough for surviving most winters in the mildest parts of Sweden. When discussing all these frost resistances it is important to note that they are only for shoots, i.e. last seasons growth and sometimes two year old growth. Nothing is known about the older stem and other organs, or their capability of taking on new growth if frost cuts them back. But considering the two *P. nivalis* here tested have been propagated from seeds produced on plants growing outside at Hörsholm arboretum in Denmark since the 1970's they are probably hardy. According to Lorentzon (1996) both species are hardy to Swedish hardiness zone 2, i.e. the mildest parts and a bit more. This is a very interesting genus with the species tested probably being the frost hardiest representatives. The hybridisation and selection work done by Graham Hutchins of County Park Nursery in England has shown there are great possibilities in this genus, and even larger growing hardy hybrids might become reality when the tested species are crossed with e.g. *P. hallii*.

Interestingly, the frost resistances recorded in shoots of reference species *Lonicera nitida* 'Elegant' and *Calluna vulgaris* 'Darkness' were surprisingly poor (see tables 6 and 7). They are both known to be hardy in southern Sweden, but were found less frost resistant than the *Podocarpus*. *Lonicera nitida* 'Elegant' can however loose branches to the frost in severe winters. It may quite possibly not have been near its potential frost resistance due to the warm winter weather (some tree peony had buds bursting in the vicinity of the shrub lending its shoots although it was mid January). The species *Calluna vulgaris* is considered the most frost resistant heather and hardy in all Sweden, while many of its cultivars are less hardy. One frost resistance earlier measured in the species was –22°C (Bannister & Polwart, 2001). The stem of *Olearia* x *haastii* was ranked between these reference species in January (see figure 7). It supports the finding that it is the most winter hardy *Olearia* grown in Britain, apart from it now being removed from the first place by *Olearia odorata*. The supposed sufficient winter hardiness in *Olearia* x *haastii* is however not proven in Sweden and therefore needs field-testing. It may for example not be sufficiently frost hardy in some essential tissues, acclimate

too late, or not tolerate prolonged freezing. The supposed parentage between *Olearia avicenniifolia* and *O. moschata* is interesting and slightly confusing considering the rather poor frost resistance measured in the latter here (stem tissues were resistant to –10.3°C in January). *O. avicenniifolia* has however been tested before by Sakai & Wardle (1978) and its frost resistance was –10°C for leaf and bud, and –13°C for cortex. Methods differed to the one here used. *Olearia avicenniifolia* is also a parent of *O.* x *oleifolia* 'Oleifolia', which was found to be the next most resistant *Olearia* after *O.* x *haastii* in January. The supposed other parent to *O.* x *oleifolia* is *O. odorata*. If this is true it is slightly odd that *O.* x *oleifolia* is the less resistant of the two hybrids. We do however not know the frost resistance in the true parents and neither do we know the effect on frost resistance when their genes are mixed.

The leaf frost resistance of *Olearia* x *macrodonta* 'Major' (–7.8°C in November and –10.3°C in January; see table 6) is in the same range as those measured for its parental species earlier: –8.4°C for *O. arborescens* and –9.6°C for *O. ilicifolia* (Bannister, 2003). The same source published a leaf frost resistance of –9.3°C for *O. nummularifolia* that is very close to the –9.2°C found in this study. Leaves of *Hebe salicifolia* showed a greater frost resistance in this study (–8.8°C in January) compared to that found by Bannister (1990): –6.0°C.

Olearia traversii is showing one of the lowest frost resistances measured, expected as it comes from the very maritime Chatham Islands far to the east of mainland New Zealand. This may be taken as additional proof of the validity of the method used. The lowland species *Coprosma virescens* was found to be the least frost resistant of those tested in that genus.

Coprosma petriei has been growing outside at Hörsholm in Denmark for decades and is obviously hardy there. The three hardier of the *Coprosma* species tested, including *Coprosma petriei*, may be said to be hardy in USDA zone 8, since they all resist –10.6 to –12.7°C. Their potential frost resistances might be even larger, but show good agreement with those found by Bannister & Lee (1989). The *Coprosma* spp. are interesting for field trials in Sweden, although these resistance figures do not bear much promise. With their large diversity in New Zealand, hybridising possibilities, and different coloured edible drupes they sure are interesting to horticulture.

There are experiences with cultivation of New Zealand woody plants in for example France, Poland, Norway, Denmark, and by Gothenburg in Sweden (see literature study: use of New Zealand flora abroad). A conclusion from these is that there are probably species of many genera that could be grown in larger parts of Europe and the more favourable parts of southern coastal Sweden, although most of those commonly grown in Britain are not sufficiently frost resistant. This need however not stop the use of more New Zealand flora in northern Europe horticulture if used in indoor gardening or for containerised plants outside in summer and protected during winter. The latter is common for several other plant groups used in northern Europe.

Plant origin and leaf size in relation to frost resistance

A positive correlation between higher mean altitudinal range and better frost resistance was found in the New Zealand plants here tested. This is not surprising and has been shown by others before (e.g. Bannister & Lee, 1989). Several studies have also shown frost resistance and winter hardiness to vary within the same species sourced at different altitudes, showing there is scope for finding hardier material of species already cultivated to improve hardiness and even extend the range where these plants can be grown. There are exceptions to the improved hardiness with higher altitude too, as shown by Harris *et al*. (2000) when *Plagianthus divaricatus* was found to be among the more frost resistant species tested in France. It is native to salt-water marshes by the New Zealand coasts. Other studies have found New Zealand plants to get more frost resistant with higher latitude, but that was not tested here.

Small leaves were dominating among the most frost resistant New Zealand species here tested, although *Olearia odorata*, which is deciduous, and the *Podocarpus* spp. mainly represented them. Small leaves were not reliably indicating high frost resistance since they were found even among the least frost resistant species. A fairer test of this would include a wide range of species from different altitudes and habitats, with several provenances of each species. A study by Darrow *et al*. (2001) has shown plants of the filiramulate habit, i.e. shrubs featuring small leaves etc., are generally not more frost resistant than larger leaved relatives. Some are though, and many of those found to be the more winter hardy in France (Harris *et al*., 2000) are possessing comparatively small leaves. *Coprosma propinqua, Corokia cotoneaster, Melicytus alpinus, Plagianthus divaricatus* and *Discaria toumatou* are good

examples. Relatively small leaves seem to be a common character of the most frost resistant New Zealand woody plants.

When looking into differences between organs within the plants, leaves were here found to be of similar or sometimes several degrees lower frost resistance compared to stem tissues, much in accordance to Sakai & Larcher (1987). It might also be worth noting that evergreen species can be prone to frost desiccation; a phenomenon separated from frost resistance. That is likely to be a problem in most of the New Zealand plants here tested unless they are protected from strong sun and dry wind while the ground or stem is frozen. The deciduous *Olearia odorata* is better adapted in that sense.

Frost resistance in November compared to January

A clear increase of frost resistance was found in the New Zealand plants from late November to mid January. Bannister *et al*. (1995) had a similar finding for New Zealand *Pittosporum*, which increased their foliar frost resistance from March and April to reach a maximum in July, corresponding to January in the Northern Hemisphere. Great increases of foliar frost resistances were also noted in New Zealand species like *Dracophyllum filifolium* and *Leptospermum scoparium* from April to August (Reitsma, 1994). The increase in this Swedish study varied from minute to several degrees, and could be quite different between leaf and stem tissues and between closely related genotypes. Material here tested is not large enough for making any certain conclusions and some variation can be explained by weaknesses in methods. The supposed variation between, and in particular within species regarding frost resistance in different organs and different rates and timing of cold acclimation would mean populations are able to rapidly adapt to differences in climate. It would also mean different aspects of cold acclimation and frost resistance could be easily selected for in breeding programs. More testing occasions and preferably controlled climatic conditions long before testing frost resistance would yield more valuable information. In this study, temperatures prior to testing in January were not significantly lower than temperatures in November. They were actually extremely mild oscillating between 4 and 10°C in January. Plants had only been exposed to one frost in early November, and there was some light frost by Christmas. These conditions might have been unusually close to New Zealand winter. It would be interesting finding out how photoperiod and temperatures affect the cold acclimation in these species. The theory of a very short acclimation period needed for species from climates with very mild

winters to attain their full frost resistance (as presented by Sakai & Larcher, 1987) may be true or not for New Zealand plants here tested. If they need a long period of cool temperatures and/or short photoperiods for full cold acclimation as preliminary indicated in this study; then it is not true.

Methods

The methods used for determining frost resistance can be discussed. First of all only one or sometimes two genotypes of a species or hybrid have been included in the test thereby not revealing the genetic variation, but e.g. Sakai & Wardle (1978) had equally low numbers. Most of the species or hybrids tested are asexually propagated and sometimes the only representatives of their kind in wider cultivation. Some of the comparisons in this report are made between potted plants and material growing in the ground. This is not ideal. Next remark is the only parts tested were outer shoots with their leaves. The outer shoots are often considered among the more frost resistant parts of plants. Achieved frost resistances might therefore give an overestimated picture of probable winter hardiness. Testing whole plants would be better since survival and regrowth could have been assessed. This, and the number or shoots (n) used per freezing treatment, was limited by plant availability. Using more shoots per freezing treatment, especially for those for which n = 3, would have yielded more accurate data overall. However accuracy would have been even better with smaller steps between the target temperatures instead of the now 5°C-decrements or more. It was a balance between number of freezers available, amount of plant material, and range of frost temperatures believed to bracket no injury, intermediate injury and large injury for all material tested.

The rate of freezing (5°C/h) was in accordance with Stener *et al*. (2002) and would be indicative of actual frost resistance for moment tested according to Sakai & Larcher (1987). In some frost resistance studies with New Zealand plants a similar rate of cooling, equal to or slightly less than 5°C/h was used (e.g., Neuner & Bannister, 1995; Bannister *et al*., 1995; Darrow *et al*., 2001). Many studies are using lower rates of freezing which would be closer to natural conditions. Many such differences of details make comparability lower between different studies.

Frost survival mechanisms are not known in most of the plants tested and probably differ between the plants. Many of the New Zealand species are probably surviving by freezing

avoidance. The relatively fast decrease in temperature might have favoured those surviving by avoidance compared to those surviving by tolerance, since a prerequisite for the tolerance strategy to work properly is comparatively slow cooling (Sakai & Larcher, 1987). Doing an exact replicate of the study could test this by decreasing freezing rate to 1°C/h. Then relative differences in frost tolerance could be compared. Adding ice to help initiate freezing in tissues (Sakai & Larcher, 1987) and keeping target temperatures for 8 h like Neuner & Bannister (1995) and others, should help prevent supercooling and show which tissues are freezing tolerant.

Electrolyte leakage and visual damage were the injury assessment methods used. Assessing the stem and leaf as single entities is actually wrong considering they are built from several tissues which might vary in frost resistance. Generalisations are however made for simplicity and have been used in numerous studies. Besides, stem tissues like cambium, phloem and xylem are often found to be similar in their frost resistance in plants from areas with very mild winters (Sakai & Larcher, 1978). Visual damage and electrolyte leakage assessment determined frost resistances were often similar but quite often differed too, with visual observations then yielding poorer frost resistance in the New Zealand plants tested. The combination of methods is however valuable for getting a more accurate and sensible picture, as discussed by Sutinen *et al*. (1992).

The visual observations should be seen as the rougher and less precise of the two methods, especially for the stem observations while leaf observations are fairly accurate. The visual observations can nonetheless be closer to the true frost resistance compared to LT_{50} from electrolyte leakage. The 50%-level of the dose-response curve from the latter does not necessarily indicate a critical point in the tissues where e.g. 50% of cells or shoots survive. The critical level where tissues can regain growth can vary for different species too, but LT_{50} is a conventional measure and the 50%-level was used here similarly to Sutinen *et al*. (1992). The dose-response curves had a sigmoid shape, as shown in many studies before. It was possible to fit the logistic function to some of these leakage data, and the LT_{50} decided from that was concluded to be similar to that from interpolation. 95%-confidence intervals was however a plus for the logistic regression. According to Verwijst & von Fircks (1994) the Richards function describing an asymmetric sigmoid curve was better describing injury data than the logistic function. They suggested the point of largest increase of injury (the derivative) in this function be used for LT_{50}. For injury data obtained in this study to be

accurately put into Richards function the quality of data needs improvement, especially with closer target temperature steps.

Dose-response curves varied largely in steepness for different genera and species. Electrolyte leakage from stem pieces of *Buxus sempervirens* 'Rotundifolia' exposed to a range of temperatures from ca –7 to –35°C expressed an almost linear relationship (but weakly sigmoidal) with leakage increasing already at –7°C and continually doing so down to the lowest temperature. *Podocarpus nivalis* was similar in response. At the other extreme are several *Olearia* with *O. odorata* showing practically no increase of electrolyte leakage until exposed to –15°C, but reaching maximum electrolyte leakage already at –25°C. Naturally frost resistance determined for species with steeper dose-response curves is likely to be more accurate. This difference of dose-response between different species certainly deserves emphasising. It can mean that some species, which are able to survive lower temperatures, are getting some damage at temperatures closer to 0°C than less resistant species. It might reflect differences in strategies to cope with frost. For species with extended and almost linear injury responses it would be interesting finding out which level is critical: which injury level should be considered their accurate frost resistance? This could be tested assessing regrowth, or using different staining techniques, in combination with electrolyte leakage.

In conclusion the methods used have several advantages including time savings compared to field trials, quantifiable measures of frost resistances, and good comparability of plants and tissues at different times of the year. The methods give a good control over events and can be useful in physiological studies of frost resistance mechanisms. As frost resistance findings in this study are found reasonable both regarding size and resultant rank of plants, the methods can be recommended for those purposes. Problems do however exist and should be kept in mind. Some of them can be found in the above discussion and in sources quoted, meaning there is great potential for improvements.

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